THE ECOLOGY AND VOCALIZATIONS OF SCOTT'S SEASIDE SPARROWS
(Ammodramus maritimus peninsulae)

By

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Since this dissertation is a formal report of my doctoral research,
it would be inappropriate for me to describe all of my ideas and my
feelings over the years--false starts, hunches that paid off, my
occasional discouragement, confusion, and elation, and even the kinship
I felt working with "my" birds on "my" marsh. But these elements were
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By

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Chairman: Dr. John William Hardy
Major Department: Zoology

   I studied the ecology and vocalizations of Scott's seaside sparrows

(Ammodramus maritimus peninsulae) in a Florida salt marsh from

1981-1985. I observed the behavior, vocalizations and reproductive

efforts of 20-30 pairs each year on the 30 ha gridded study site. These

monogamous birds defended all-purpose territories about 1,750 m^2 in size

with song and short-distance agonistic behaviors. A high proportion

of males (0.79) returned each year to their previous territories, and

half (0.50) of these remated with their previous year's mates. Although

females initiated about 3.7 clutches of 3 eggs each season, productivity

was low (0.67 fledglings/female/year), because predators destroyed about

80% of the nests. Nevertheless, population numbers remained stable over

the years 1979-1985. The birds' vocal repertoires consisted of a

primary song, three modified primary songs (whispering song, flight

song, and subsong), and 10 calls. Only males sang; they had a song

type repertoire of 2-3 songs. I experimentally investigated the

function of song during the breeding seasons of 1983-1985 by temporarily

muting male birds in the field. I muted birds by rupturing the interclavicular air sac. Birds remained songless for about 2 weeks but could give all of their normal calls during this time. I administered two rounds of mutings, each preceded and followed by time budget, playback, and other observations on 3 treatment groups: Muted, Sham-Operated, and Undisturbed birds. The Early muting round tested for mate and territory acquisition. These Muted birds remained mateless until they regained their voices; most eventually attracted a mate. Muted birds acquired territories later than Sham-Operated and Undisturbed birds. The Mid-Season muting round tested for mate and for territory retention, and changes in behavior. All Muted birds lost their mates; a few attracted new mates when they regained their singing ability. Their territories either shrank or were lost, but new territories were established (or the original re-expanded) when singing ability returned. The intensity of close-range aggressive behaviors was significantly greater for Muted birds than for Sham-Operated and Undisturbed birds. There were no discernible differences between Sham-Operated and Undisturbed birds for any of the attributes measured.

CHAPTER I
GENERAL INTRODUCTION

I studied the ecology and vocalizations of Scott's seaside sparrows (<u>Ammodramus</u> <u>maritimus</u> <u>peninsulae</u>) on a salt marsh near Cedar Key, Florida, for 5 years. William Post had studied the reproductive ecology of this population from 1979-1980. In early 1981, I began my investigations and continued my study through the spring of 1985. The principal objective of my research was to determine the function of the vocal repertoire of these birds. During the course of my field work, however, I observed many aspects of their biology and also collected reproductive and non-vocal behavioral data.

This dissertation summarizes both my observational and experimental investigations of the study population. Chapter II is an overview of the project history, study site, general methods, and the birds and their biology. Chapter III describes the vocal repertoire and discusses the probable function of these vocalizations. Chapter IV summarizes the experiments I conducted in 1983 and 1984, whereby I determined the function of song in Scott's seaside sparrows.

The information presented throughout most of this dissertation portrays the behavior of birds I observed and tape recorded with a minimum of disturbance. The exception, of course, is that Chapter IV presents results of manipulative experiments. Thus I sometimes make the distinction between "normal" and "experimentally manipulated" birds.

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NATURAL HISTORY AND BEHAVIORAL ECOLOGY OF SCOTT'S SEASIDE SPARROWS:
STUDY TECHNIQUES AND RESULTS

Taxonomy and Morphology

Seaside sparrows (<u>Ammodramus maritimus</u>) belong to the "grassland
group" of Emberizine finches (subfamily Emberizinae), which also
includes the genera <u>Ammospiza</u> and <u>Passerculus</u>. The nominate form (<u>A</u>. <u>m</u>.
<u>maritimus</u>) was originally described by Wilson in 1811. Currently nine
subspecies of seaside sparrows are recognized (American Ornithologists'
Union [A.O.U.] 1957, 1973), including the nearly extinct dusky seaside
sparrow (<u>A</u>. <u>m</u>. <u>nigrescens</u>). Beecher (1955) postulated that formation of
the races of seaside sparrows was due primarily to geographic isolation
caused by post-glacial rise in sea level and the concurrent drowning of
river mouths forming bays (also see Funderburg & Quay 1983). All but the
southernmost populations of the nominate race are migratory. The other
races are generally considered to be non-migratory.

Scott's seaside sparrow (<u>A</u>. <u>m</u>. <u>peninsulae</u>) was named in honor of W.
E. D. Scott and described in 1888 by J. A. Allen. The type specimen was
collected near Tarpon Springs (Pinellas County, Florida). <u>A</u>. <u>m</u>.
<u>peninsulae</u> ranges from Old Tampa Bay (Hillsborough County, Florida)
north to Pepperfish Key (Dixie County, Florida) (A.O.U. 1957).

Austin (1983) and I (McDonald 1983a) have briefly discussed and
annotated the taxonomic history of the seaside sparrow assemblage. The
distinguishing plumage color characteristics of the seaside sparrow
subspecies are thoroughly described and compared by Funderburg and Quay

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(1983). Three museums in the United States house good representative collections of seaside sparrows that I have examined: The American Museum of Natural History, the United States National Museum of Natural History, and the Florida State Museum.

Seaside sparrows are generally recognized by their dark gray-brown head and body (total length about 14 cm), narrow black streaks on the breast and flanks, yellow lores and wrist spots, and long bills. The tail is relatively short and narrow and the feet and legs are relatively large, in proportion to the size of the bird. When flushed, seasides characteristically fly short distances and then drop back into the marsh vegetation. Unlike other sparrows, seaside sparrows eat many crustaceans and insects, but few seeds.

In his original description, Wilson succinctly described seaside sparrow habits when he said: "Amidst the recesses of these wet sea marshes, [the bird] seeks the rankest growth of grass and sea weed, and climbs along the stalks of the rushes with as much dexterity as it runs along the ground, which is rather a singular circumstance, most of our climbers being rather awkward at running" (Wilson 1811, p. 68).

Scott's seaside sparrows are among the darkest of the seaside sparrows. As in other races a certain degree of individual color variation exists. Some birds approach the lighter colored A. m. maritimus in shading on the dorsum; others approach the darker A. m. nigrescens. Early taxonomists made no mention of this color variation, although Griscom (1944) recognized it. Austin states: "A gradual cline is evident from the smaller, grayer populations in the south (peninsulae) to the slightly larger, darker, and dorsally browner birds in the northwest corner of the range in the Wakulla area (juncicola)"

(Austin 1968a, p. 838). However, W. Post and H. W. Kale (pers. comm.), most familiar with the morphological variations in the southern subspecies, agree that there are apparently no characteristics consistently separating A. m. peninsulae and A. m. juncicola (Wakulla seaside sparrow). The range of juncicola is contiguous with peninsulae near Pepperfish Key, Florida and extends to southern Taylor County, Florida. Thus, juncicola should probably be merged with peninsulae, which has taxonomic priority.

In all seaside sparrows the sexes are identically colored, but males are slightly larger. In my study at Cedar Key I routinely took wing length (wing chord) and weight measurements. For adult males and females the mean wing chord measurements and 95% confidence intervals were 58.9 (+0.4) mm and 54.0 (+ 0.3) mm; and mean weights 22.5 (+ 0.6) g and 19.6 (+ 0.7) g, respectively (N=134 males and 78 females). Thus females were 93% as large as males based on wing chord measurements and 89% as large based on weight measurements. Because the 99% confidence intervals for wing chord did not overlap, male and female adults handled outside of the breeding season could be sexed using wing chord. During the breeding season the age and sex of birds could more easily be determined using other criteria. Females possessed a vascular, edematous brood patch about 1.8 cm wide and males had a cloacal protruberance of about 2 mm. Fledglings and older hatching-year birds had a characteristic paler plumage pattern.

Project History and General Methods

The study site near the Gulf coast town of Cedar Key, Florida, was established by William Post in December 1978. Post investigated the

habitat and reproductive biology of the birds for two years, under
contract with the Endangered Species Program of the Florida Game and
Fresh Water Fish Commission. Information and results obtained from his
project were to become part of a management plan for the rare and
endangered Atlantic coast population of A. m. nigrescens. Post gridded
the marsh with stakes, began color banding of birds, mapped vegetation,
sampled the invertebrate fauna, studied the interspecific influence of
fish crows (Corvus ossifragus) and rice rats (Oryzomys palustris) on
sparrow reproduction, and recorded other descriptive data pertaining to
the morphology and life history (Post 1980, 1981a, 1981b; Post &
Greenlaw 1982; Post et al. 1983; Greenlaw & Post 1985).

Post concluded his field work in the summer of 1980. I accompanied
him to the study site several times early in 1981, and then assumed
responsibility for the study site and birds later in the spring of 1981.

During the breeding seasons (March-June) of 1981-1982 I familiarized
myself with the marsh and the birds' behavior, and continued color
banding adults and some nestlings. I spent an average of 50 days in the
field each of these two years, observing and tape recording
vocalizations.

In 1983 and 1984 I continued comprehensive observations and color
banding of my Florida study population, each year averaging about 70
days in the field from March through June. Behavioral observations on a
field day consisted of 2-4 hours of watching, recording some of the
vocalizations, and describing behavior and territories. I recorded
spoken notes on a tape recorder, and included the location of birds and
activity time (measured with a stopwatch). I later transcribed tapes
and analyzed the data.

The major investigation of my study--temporary song muting--was conducted during the breeding seasons of 1983-1984 and is described in Chapter IV. In the spring of 1985 I spent 15 days in the field censusing returning and new males and conducting playback experiments with female seaside sparrow vocalizations.

Throughout this report the data designated as having been collected in 1979-1980 are from Post's unpublished and published work and are used with his permission. All other data were collected and analyzed by me. I used non-parametric statistical tests (Siegel 1956; Conover 1980) for most analyses.

Study Site

General Description

The 30-ha salt marsh study site was north of the Waccasassa Bay of the Gulf of Mexico. The site was 6 km NNE of the town of Cedar Key, Levy County, Florida, and within the Sumner Quadrangle, USGS Map (29° 11' N, 83° 00' W). The physical boundaries of the marsh, exterior to the core gridded study area, were Prodie Creek on the SW, Live Oak Key and Waccasassa Bay on the S, and Dorset Creek on the NE. The property was privately owned.

The boundary between the marsh and Waccasassa Bay was not sharply defined. The shoreline was dotted with oyster bars and many small islands and was cut by numerous tidal creeks. Except for these creeks, which ranged from 0.5 to 1.5 m deep at mean high tide, the marsh was flat. Tides averaged 0.8 m. Most years one or two flooding episodes occurred during the breeding season, destroying any existing nests of seaside sparrows. These floods were most often generated by prevailing

winds from the south, driving water in from Waccasassa Bay, combined
with a natural (high) spring tide event. The water level during these
floods usually rose about a meter above mean high tide. Average salinity
measured by Post (1980) at 32 stations on 24 April 1980 was 19.03 $\pm$ 1.09
0/00.

Weather

Data on cloud cover, air temperature, and wind direction and
velocity were collected at about hourly intervals throughout each field
day. Phenological records such as flowering dates and spring migration
observations were also kept. More complete daily weather information
(maximum and minimum temperatures and rainfall) for all years was
recorded by a National Oceanographic and Atmospheric Administration
(NOAA) station near the town pier of Cedar Key.

My behavioral observations and the handling of birds were carried
out under mild weather conditions ($18-33^{\circ}$ C, wind <20 km/h) during the
months of February through June. During my 5-year study, however, I did
visit the marsh in all months of the year and under virtually every
weather condition. Temperatures I recorded ranged from 3° C (January) to
41° C (August). On typical sunny days during the height of the breeding
season (April and May) the mid-morning temperatures averaged 26° C. For
those field days on which I took detailed behavioral observations, the
wind velocity usually ranged from about 2 km/h (just prior to sunrise)
to about 12 km/h by 0900, and then 16-24 km/h by early afternoon.
Prevailing winds were mostly from the southwest. A few sultry field
days were virtually windless. Winds approaching gale force (50+ km/h)
occurred occasionally in the spring and fall.

In September 1985, Hurricane Elena touched the Cedar Key area. My
surveys the following week and in 1986 indicated no discernible
population decline in the three bird species breeding on this marsh
(seaside sparrows, marsh wrens [Cistothorus palustris], and clapper
rails [Rallus longirostris]).

Marsh Fauna

Vertebrate fauna

The six-year average population densities of the three resident
bird species were seaside sparrows--2.5 $\pm$ 0.1 birds/ha, N=253; marsh
wrens--0.6 $\pm$0.3 birds/ha, N=23; and clapper rails--0.5 $\pm$ 0.1 birds/ha,
N=59 (Post 1981a; McDonald 1982, 1983b, 1984, and my unpublished surveys
for 1984 and 1985). In addition to these residents, migratory
sharp-tailed sparrows (Ammodramus c. caudacutus) wintered on the marsh.
They regularly arrived in the last week of September and left in the
second week of May. The population density of sharptails averaged about
2/ha. Other bird species seen foraging or resting on the study site
were those commonly found in Florida Gulf Coast salt marshes (Post
1981a; McDonald 1982, 1983b, 1984).

As described below in the section on reproduction, most seaside
sparrow nest losses were attributed to predation, primarily by fish
crows and rice rats. The rice rats dwelt on the marsh. Their density was
about 8/ha (Post 1981b). I also found evidence of predation by
transient racoons (Procyon lotor).

Other species of mammals were occasionally observed: river otters
(Lutra canadensis) played on the bank edges; Atlantic bottlenose
dolphins (Tursiops truncatus) and very rarely, manatees (Trichechus
manatus) swam in the larger tidal creeks. The only reptile I saw on the

study site was the Gulf Salt Marsh Snake (Nerodia fasciata clarki), observed on three occasions.

Invertebrate fauna and seaside sparrow foraging.

The most obvious and abundant invertebrates on the marsh were fiddler crabs (Uca rapex) and Gulf periwinkles (Littorina irrorata). Genoni (1984) reported additional mud-inhabiting invertebrates from this marsh. Terrestrial invertebrates were also censused previously by sweep-netting the vegetation during the sparrows' breeding seasons (Post et al. 1983). By percent of total sample, these were Tettigoniidae (54.3%), Lycosidae (18.8%), other spiders (7.8%), and Lepidoptera (Noctuidae and Pyralidae) (3.0%). Six additional invertebrate families each represented less than 5% of the total sample. Post et al. (1983) found that 85% (by volume) of the nestling's diet consisted of these 10 groups of arthropods.

The invertebrate food species consumed by adults on this marsh are probably nearly the same as those eaten by Scott's and other subspecies of seaside sparrows on similar marshes. Howell (1928, 1932), Oberholser (1938) and Wilson (1811) examined stomach contents of adult Scott's, Smyrna (A.m. pelanota), Louisiana (A. m. fisheri), and dusky (A. m. nigrescens) seaside sparrows. In addition to the arthropod groups listed above, which are known to be fed to nestlings at Cedar Key (and presumably eaten by adults), these authors found adults had eaten marine "worms," small crabs and other crustaceans, beetles, dragonflies, flies, wasps, bivalves, gastropods, and some "weed" and grass seeds. (Audubon [1831] said that a pie he made of seaside sparrows could not be eaten due to its "fishy savour," surely attributable to the birds' having consumed mostly salt marsh invertebrates!)

With the assistance of a biologist familiar with marsh invertebrates, I examined the stomach contents of eight adult birds from my study site. Surprisingly, three of the stomachs were virtually empty. These males had died early in the morning during the breeding season, perhaps prior to foraging. The other stomachs contained mostly arthropod exoskeletons (fragments of crabs, insect adults and pupae, and one small spider), snails (Pyramidellidae and Marginellidae), and vegetation. Post et al. (1983) presented convincing evidence that food was plentiful and accessible to the Cedar Key birds throughout the year.

I rarely observed birds drinking. Several times I saw then imbibe dew from the vegetation, and once I saw a bird drinking and bathing at the edge of a shallow tidal creek. Although no passerines have salt glands, seaside sparrows do have the ability to concentrate urine when consuming salt water (Poulson 1969).

Marsh Flora

Vascular plant species on the study site were described in detail by Post (1980). In order of relative cover, the major plants were smooth cordgrass (medium height) (Spartina alterniflora) 38%, black rush (Juncus roemerianus) 26%, seashore saltgrass (Distichlis spicata) 23%, and perennial glasswort (Salicornia virginica) 8%. There were no woody plants within the gridded portion of this marsh. Also, there were no pannes (bare mud areas devoid of vegetation) until September 1985, after the passage of Hurricane Elena near the Cedar Key region. Apparently some stands of Spartina were submerged for at least several days during the storm; consequently these drowning-susceptible plants died.

Size and Demarcation of Study Sites

Post established two contiguous study areas, Cedar Key West ("CKW," 10-ha in area) and Cedar Key East ("CKE," originally 20-ha in area). Although CKW and CKE were contiguous, the study populations of seaside sparrows living on each site were separated by 200-400 m, and the populations did not interact. Both study areas were gridded with 2-3 m high wooden stakes placed at 25 m intervals. Stiff metal prongs on the tops of the markers discouraged their use by predatory birds. Stakes were alpha-numerically designated and could be read from at least 50 m. Additional markers were placed around the peripheries of the study areas for reference. I concentrated my preliminary observations on the CKW birds in 1981, then switched to CKE study area (which I enlarged to 30-ha in 1984) for the remainder of my project.

Reproduction and Reproductive Behavior

Overview of Annual Cycle

Fig. II-1 graphically summarizes the reproductive cycle of Scott's seaside sparrows at the Cedar Key study site. The cycle commenced in early March with the onset of regular singing by males and subsequent territorial establishment and mate acquisition. The peak of the breeding season (as indicated by the number of newly completed clutches) for the six years 1979-1984 occurred during the second and third weeks in May. In a typical spring the first clutches were completed around the beginning of April, and the last clutches by the end of June. Most clutches (85%) were completed by the end of May. Virtually all breeding and territorial defense activites ceased by mid-June. Both

adults and juveniles entered a prolonged molting period during the early fall and remained difficult to observe until the following early spring.

Figure II-1. Breeding chronology of seaside sparrows at Cedar Key, Florida, 1979-1984. Data from Post 1980; Post et al. 1983; and author's unpublished observations. Bars represent proportions of total sample of 293 nest observed during indicated 2 week intervals.
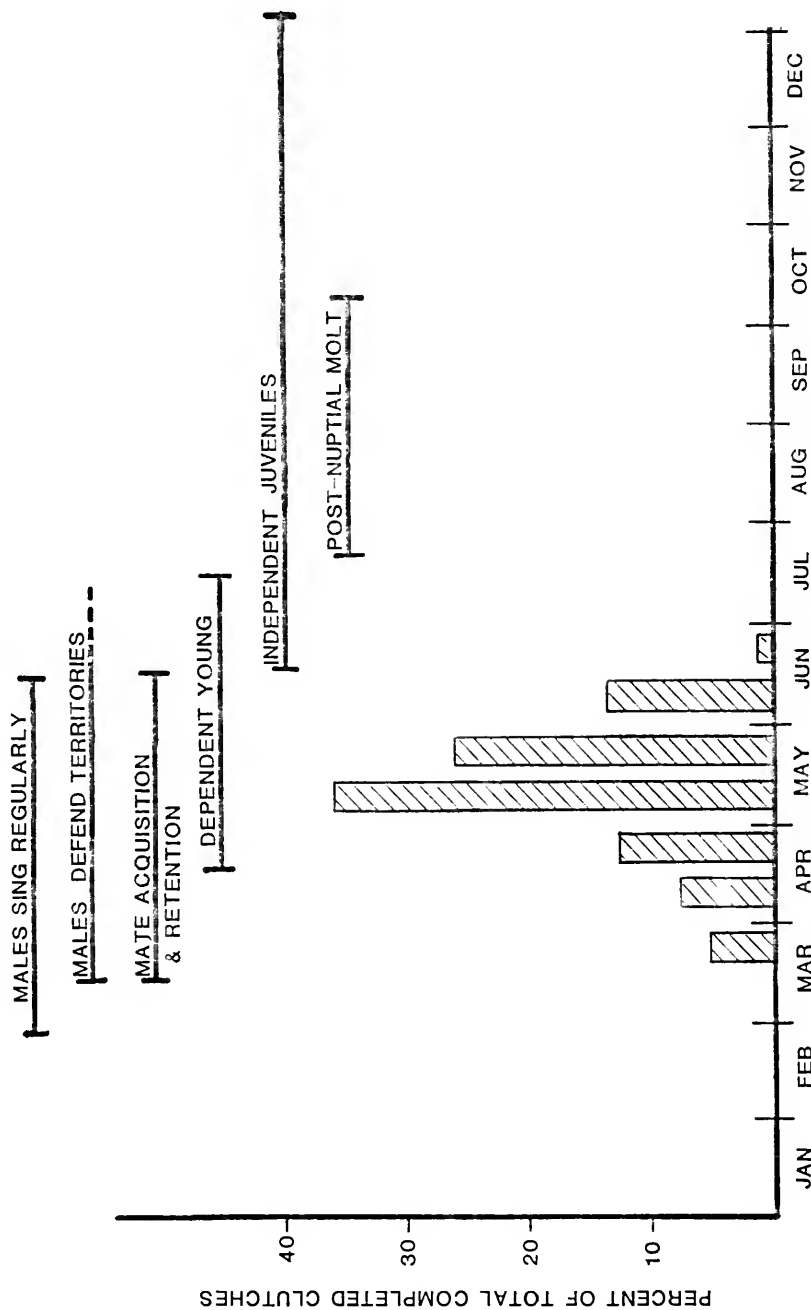
Annual Cycle of Reproductive Behavior

Territorial establishment and mating

Breeding behavior of Scott's seaside sparrows near Cedar Key began in late winter (February) with sporadic singing of adult males on warm, windless mornings. Young adult males, hatched the previous spring, also began to sing imperfect subsongs. By early March all males were singing typical primary songs, and females began to associate with males. Females solicited male affiliation with the "whinny" and "tcni" calls (Chapter III).

During these early weeks of the season, weather influenced the intensity of singing and other observable breeding activities. Wind velocities greater than 25 km/h accompanied by temperatures less than 20° C caused a nearly complete cessation of overt territorial and mating behaviors. Mild weather, even in early February, greatly enhanced regular singing activity and behavioral interactions. In addition to this immediate influence of atypical weather, prolonged cool temperatures delayed the onset of breeding within a given season, and hot weather in late May caused an early cessation of breeding activities. The early spring of 1983, for example, was unusually cold: average daily temperatures for March were about 5° C below normal throughout mid-Florida. The breeding activities of the study population at Cedar Key were about 2 weeks delayed that year--I did not find a completed clutch until 26 April. On the other hand, the unusually warm February of 1985 certainly must have accounted for my finding fledged seaside sparrows on 16 March and fledged marsh wrens on 23 February, both record early nesting dates for these species for any known breeding locality.

Most males re-established the same territories from year to year and vigorously defended these during March and early April, the period when the most fervent territorial disputes between first-year and older adults and between residents and floaters broke out. By May territorial ownership and boundary disputes were rare, seemingly occurring only when floaters attempted (always unsuccessfully) to take up residence on an occupied territory. The intensity of singing (as measured in minutes of singing/hour) also declined gradually after a peak in early April. By June there was only sporadic singing activity occurring daily from just before sunrise to about one-half hour after sunrise.

Most birds paired by mid-March. The mates remained paired over the remainder of the breeding season. I never observed a natural incidence of divorce, although Werner (1975) reported several instances of re-pairing in his Cape Sable birds in the same breeding season. Seven percent of 97 non-experimental territorial males remained bachelors throughout the breeding season in my study. Werner (1975) reported that about 12% of his 111 Cape Sable seaside sparrows were bachelors. Apparently the adult sex ratio of the breeding birds was slightly skewed in favor of males. Although Post (1980) assumed that most unmated territorial males were probably first year birds, my longer study of these marked birds indicated no significant difference in the proportions of unmated older territorial birds and unmated first-year territorial birds ($\underline{X}^2$=0.4, N=10 bachelors, df=1, $\underline{P}$>0.5).

My observations over the years also suggested that returning males tended to re-mate with their female of the previous year, if she also returned the second year. I documented mate retention using data for non-experimental males and females present in both 1983 and 1984, the

years for which I had the most complete data. Of the 10 cases in which both members of the pairs were present in succeeding years, there were five re-mates. Mate retention from year-to-year also occurs in northern seaside sparrows on Long Island, New York (Jon Greenlaw, pers. comm.). Werner (1975) also stated qualitatively that there was some degree of year to year mate retention in his Cape Sable seaside sparrow subjects.

Females solicited copulations with a slow, low-pitched variation of the "whinny" vocalization accompanied by quivering bilateral wing raises. This display was given at ground level with the bird concealed in the marsh vegetation. A nearby male (usually the mate) was immediately attracted to this enticing behavior and would quickly copulate by mounting the female briefly with fluttering wings and then bounce off, landing several meters away. The male sometimes gave one or two songs immediately after copulation, whereas the female was almost always silent afterwards.

Typical bouts of copulation involved three to five mounts during time intervals of 0.5 to 1.5 hours. All of the copulation bouts I observed occurred in the mornings. During this period the female sporadically gave her solicitation whinny, while the male remained within a 15 m radius of her and sometimes sang. Of the 96 copulation bouts I observed under non-experimental conditions, all but three were between birds I had previously known or subsequently knew to be mates. On the remaining three occasions I observed neighbor or floater males sneak in and copulate with a soliciting female while the mate was vigorously singing or confronting other birds on the opposite side of his territory.

Nests, eggs, and early development

Although this was primarily a behavioral study, nesting and other reproductive data were routinely collected during the breeding seasons of 1981-1984, and in some cases were consolidated with Post's 1979-1980 data.

Seaside sparrow nests are notoriously difficult to find in salt marshes. My early efforts to find nests by dragging a chain through the vegetation, by trying to flush nesting females by walking transects, and even by using a bird dog were largely unsuccessful. I eventually learned to locate most of the nests of subject birds by close observation of the parents.

For all nests I found, I noted date and time of discovery, parents, location relative to the grid system and territorial boundaries, and vegetative microhabitat. Because I wished to minimize human interference, I handled only a sample of the nests and nestlings that I was aware of. The additional information taken for these sample nests was form of nest cup (open or domed), height from ground to bottom of cup, dimensions of cup (inside and outside diameter, inside and outside depth), material used in constructing nest, number of eggs or hatchlings, egg dimensions, hatchling weight (for 11 individuals), age of hatchlings, and daily survival. I also weighed seven nests collected after fledging.

The following summarizes my descriptive data on 194 nests. Two nests had well-defined domes and entrances. I detected no preferred directional entry pattern of attending parents for any of the nests, although the nests of some subspecies of seaside sparrows are mostly domed and have distinct entrances. About half of the nests were built

in _Distichlis_ and the remaining roughly split between _Salicornia_ and _Juncus_ microhabitats. All nests were constructed primarily with the _Distichlis_ grass; a few had small _Spartina_ leaves woven in. The average height of the nest (as measured from the ground to the bottom of the nest cup) was 35 cm. Average nest size measurements were: outside diameter of cup 9.3 cm; inside diameter of cup 5.4 cm; outside depth of cup 5.3 cm; inside depth of cup 3.3 cm. Also in contrast to other subspecies, at Cedar Key the average clutch size was smaller (3.02 $\pm$ 0.17 eggs, N=194 nests), compared to about 3.65 in New York (Post et al. 1983).

Average egg dimensions were 20.6 mm X 15.7 mm (N=35), and egg weights averaged about 2 g. While exhibiting minute individual variation, the color pattern of the eggs was essentially the same as described for seaside sparrows in detail elsewhere (Austin 1968a).

Egg and nest cup dimensions for Scott's seaside sparrows at Cedar Key were within the ranges reported for other subspecies in the literature (Austin 1968b; Norris 1968; Sprunt 1968; Trost 1968; Woolfenden 1968; Werner 1975; Greenlaw pers. comm.) and in collections I measured at the American Museum of Natural History, the United States Museum of Natural History, and the Florida State Museum.

I categorized nest placement within a pair's territory as "edge" or "center." An edge nest was so designated if it was built in the outer fourth of the total area of the territory. I found no significant difference in the birds' tendencies to locate nests at the territory edge versus towards the center ($\underline{X}^2$=0.7, N=194, df=1, $\underline{P}$>0.4).

Only 116 nestlings were directly observed, but others were known to be in active nests. The young remained in the nest 9-11 days. Their

weights increased from 2.2 g on Day 0 to 15.1 g on Day 10. The few other morphological data I took on these birds agree with Werner's (1975) extensive quantitative morphological data and photographs of nestlings taken days 1-8 for Cape Sable seaside sparrows.

Norris (in Austin 1968a) gave a detailed description of nestling Louisiana seaside sparrows (A. m. fisheri) and the behavior of the young and their parents. My observations of Scott's seaside sparrows at Cedar Key are very similar to Norris's in Louisiana.

Nesting behavior

Nest building (by the female only) began on the day of or the day after copulation bouts. Females did not re-use nests, but built a new nest for each new clutch. The female usually completed building her nest within a day and laid her clutch of three eggs (rarely four) over the next five days. The eggs were laid one a day, at any time during the day. Infrequently females that were building nests, laying, or incubating, would copulate with their mates. Incubation was by the female only, for 11-12 days.

Most years the first young of the season hatched around the second week in April (Fig. II-1). All of the young hatched within 24 hours and began to gape and utter soft "peeps" on the day of hatching. The eyes were fully opened by day five and at about this time the begging vocalizations changed from a "peep" to a "churp" and became more intense. Some nestlings fledged and were able to run about as early as Day 9. Most began short flights about Day 13.

The hatchlings remained in the nest for 9-10 days and were fed by both parents. The combined average feeding rate was 3.2 visits per hour. Parents also maintained a clean nest by removing fecal sacs. Post

et al. (1983) determined the diet of hatchlings older than 3 days by placing pipe-cleaner ligatures around their necks and then removing the food from the young or the nest cups after an hour had elapsed. The most important food groups for the nestlings were found to be the insects of the taxa Tettigoniidae and Lepidoptera and spiders of several families. These invertebrates constituted 85% of the nestlings's diet.

Both parents continued to feed the young for 15-20 days after fledging. If the breeding season had not progressed too far (i.e. prior to about 15 May), a female with fledged young would begin to renest about a week after the first brood had fledged and would leave the care of fledglings to her mate. I noted five such cases in 84 pairs.

Since most nests were destroyed before young fledged, seldom did a pair actually have the opportunity to rear a second brood within a season. From late March through early June, unsuccessful parents would try repeatedly to raise a family. The average number of nesting attempts per season of 84 pairs (1981-1984) was 3.7, and the interval between nest destruction and renesting was 5.7 days. In 1984 I observed one pair attempt seven nests, all unsuccessful.

Fathers began to avoid their first brood after tending their fledglings for about three weeks, or after their second successful clutch hatched. They chased their fledglings (as well as any other juveniles) off the parental territory and started to devote their attention to their new brood. After nesting had stopped family groups of fledged, dependent young and their parents were often observed during the months of June and July. Adults without families were seldom seen during this period, especially during the hot daytime hours.

Post-Breeding behavior

By August most juveniles were independent and began to form loose groups of about three to eight. Sometimes adult males associated with these groups, which persisted through October. Juvenile males gave occasional bouts of imperfect subsong in August and September, and rarely through the winter. Although present (as evidenced by occasional mist net captures), adult females were rarely seen in summer.

From late September through October there was a resurgence of easily observable but essentially non-vocal behavior, such as foraging and territorial defense. From these observations and my intensive mist netting in the fall of 1982 and 1983, I concluded that adult males and females remained within a radius of about 250 m of their previous spring territory throughout the year. Juveniles appeared to wander a great deal more, perhaps as far as several km.

Little is known regarding the fate of the fledgling seaside sparrows at Cedar Key or elsewhere. Of the total of 98 hatchlings and fledglings Post and I banded at Cedar Key, I recaptured only 4 during my intensive netting 1982-1984. Presumably the emigration and general mobility of fledglings as well as of non-territorial older birds are mechanisms for the birds' locating and colonizing any unoccupied territories and viable habitat.

The Cedar Key population appeared stable (average density 2.5 birds/ha) throughout the 7 years 1979-1985. Adult birds with territories were relatively long-lived. By the end of 1984, I had studied subject males from 1 to 4 years. According to banding records, two males were at least 5 years old, and one was at least 6 years old.

The adult post-nuptial molt (and only annual molt) of their nuptial plumage began in early July, and the post-juvenile molt began in late July. Both molts were completed by October.

The seasonal weight variation was slight but significant. Both sexes were heavier in winter than in summer, but the difference was not as great as in the nominate migratory seaside sparrows (Post 1980).

Productivity, Survival, and Reproductive Success

I summarized parameters of reproduction for seaside sparrows at Cedar Key in Table II-1. The data combine my unpublished observations (1981-1984) with Post's observations (1979-1980), as given in Post 1980 and Post et al. 1983.

Post (1981b) intensively studied seaside sparrow reproduction and factors that affected productivity during his 1979-1980 project. He also compared these characteristics of reproduction in A. m. peninsulae to another well-studied population, A. m. maritimus in New York (Post & Greenlaw 1982; Post et al. 1983). I combined the two years of Post's data with reproductive data I collected 1981-1984.

Studies of nest productivity should consider whether nest failures are due to human disturbance. I did not test if my visitations affected the nesting success I observed. Post (1980), however, did test for an observer effect using the methods of Mayfield (1975) and Johnson (1979) and found that the frequency of nest visitation did not affect nesting success of Scott's seaside sparrows.

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Table II-1. Summary profile of territoriality and reproduction of
Scott's seaside sparrows at Cedar Key, Florida, 1979-1984

Territories, Mating, and Return Rates[a]

Mean territory size	$1759 \pm 242 \text{ m}^2$
Ecological density of territorial males	2.5 males/ha
Mean annual return of territorial males	0.78 males/yr
Proportion of re-mates[b]	0.50
Proportion of bachelor territorial males	0.07
Ratio unmated first year/older males[b]	4/6 N.S.
Mean length of study of male in population	2.3 yr

Productivity and Survival[a,c]

Mean clutch size (C)	3.02 ± 0.17
Mean no. clutches initiated/female/yr (I)	3.7
Probability of egg producing fledgling (S)	0.06
Productivity (fledglings/female/yr)[b]	0.67
Mean length of breeding season	95 days
Proportion of nests producing fledglings	0.06
Nest success ratio of young/older breeders	3/5 N.S.
Adult annual survival (male return) rate	0.78
Juvenile survival rate[b]	0.67
Production of fledglings->breeders next yr[b]	0.45/female/yr

[a] Combined data from Post 1980; Post et al. 1983; and author's
unpublished observations. Probability level: N.S.=P>0.05.

[b] See text for explanation of calculations.

[c] Based on 194 nests

At Cedar Key the probability that a nest would produce fledglings was remarkably low, but because females renested within 7-8 days of nest destruction, the population seemed to have remained stable from 1979 through 1985. That is, bird density remained about the same over the years we censused the study population (Post 1980, 1981a; McDonald 1982, 1983b, 1984, and my unpublished data).

Post et al. (1983) calculated probability of an egg's surviving 21 days (through the egg and nestling period) and producing a fledgling to be only 0.06 (Post et al. 1983). This contrasts with an egg survival rate of about 0.35 in New York.

Of a total (McDonald and Post) sample of 194 nests whose fates were carefully documented, only 12 (6%) produced at least one fledgling. The major causes of nest mortality at Cedar Key were flooding, and predation by fish crows and rice rats. Eight (4%) of the nests failed due to desertion. Neither Post nor I ever suspected hatchling death due to starvation. I found only a few instances of partial nest mortality. Eleven (2%) of the 473 eggs I observed in the field failed to hatch and were presumably infertile.

Destruction by flooding accounted for the mortality of 17 (9%) of the nests. Normal tidal fluctuations in water levels seldom reached the bottom of the nest cup (about 35 cm above the ground). However, in most years at least one major unpredictable flooding of the marsh occurred. For the seven years (1979-1985) there were nine such floods during the breeding seasons.

Predation by fish crows destroyed 37 (19%) of the total nests. Fish crow predation was assumed when eggs disappeared without leaving shell fragments or a disturbed nest (indications of mammalian predation). Fish

crows were about three times more likely to prey upon nests with hatchlings than on those with eggs.

Post (1981b) concluded that nesting in Juncus should be preferred by the birds because Juncus stands were less likely to be flooded and because this vegetation provided cover protection from fish crow predation. However, rice rats on the marsh apparently discouraged seaside sparrows from nesting more in Juncus by destroying their nests (Post 1981b). The birds were found to nest more frequently (85% of the total nests) in less dense Distichlis and Salicornia, even though nest failure was more likely to occur in these vegetation types, as compared to failures in Juncus (Post 1981b).

The remaining 120 (62%) of the total nests were destroyed by rice rats and unknown predators (probably racoons).

Post (1981b) tested whether rice rats were actually destroying nests by placing tin cylinders around nests. These were open at the top, allowing entry by parents and aerial predators but excluding small mammals. Forty-eight percent of 42 experimental nests with this protection produced fledglings, whereas only 6% of the 34 control (unprotected) nests had young that fledged.

To summarize: about 80% of the nests at Cedar Key were destroyed by predation. This contrasts with findings in New York where fewer seaside sparrow nests were destroyed by predators and more losses (about 65% of the total nest mortality) were due to flooding or rains, desertion, hatching failure, and unknown causes (Post et al. 1983).

I report productivity as the number of fledglings/female/year. Post's data (1980) were combined with mine: Post observed 109 clutches, and I observed 85 clutches. Productivity was determined by the method

of Ricklefs and Bloom (1977): Productivity = Mean Clutch Size (3.02) X Probability of Egg Success (0.06) X Number of Clutches Initiated by a Female/Year (3.7). (The term "productivity" and its values are roughly equivalent to the "realized specific natality rate" parameter that is conventionally calculated using life table data.) The six year average productivity for 1979-1984 was 0.67 fledglings/female/year. This value contrasts with the much higher rate of 4.25 for the New York population. New York females produced about six times as many young within their average 75 day breeding season as the Florida birds did in their average 95 day season. The annual survival, however, was lower in New York (Post et al. 1983).

I determined the adult annual survival rate at Cedar Key to be about 0.78, based on the return of 51 of 65 adult males over the years 1980-1983 and assuming a roughly equal sex ratio. This figure represents a minimum value, since some birds may have emigrated. This is a relatively high value for a small Passerine bird. Werner (1975) estimated a 0.88 survival rate for the likewise non-migratory A. m. mirabilis, based on a one year return sample. Adult survival is lower for migratory A. m. maritimus--only about 0.45 (Post 1974).

I estimated the juvenile survival rate to be about 0.67. This figure was determined using the method of Post et al. (1983) and using their estimated ratio of juvenile/adult survival (0.85, as determined from returns of banded nestlings and adults). Thus, I multiplied the adult annual survival rate of 0.78 by the ratio of juvenile/adult survival of 0.85, giving 0.67.

Although I did not have enough data to directly calculate net reproductive rate (R_0) using life table parameters, I suggest that the

Cedar Key population of seaside sparrows is maintaining its numbers for the following reasons: First, there was no decline in population density over the years. Additionally, my experiments in 1983-1984 demonstrated that floaters (itinerant males without territories or mates) were always available to take up residence on territories they perceived as unoccupied. Secondly, the reproductive data I do have suggest that enough juveniles were produced and survived to replace non-returning adults. That is, using my calculated productivity figure of 0.67 fledglings/female/year and Post's (1980) juvenile survival rate of 0.67, each breeding female (pair) produced 0.45 first-year birds. Assuming a sex ratio of about unity, each female produced 0.225 first-year female breeders. If the minimum adult annual survival rate was 0.78 and applicable to both sexes, then the annual adult female mortality rate was 0.22 (1.00 - 0.78 = 0.22) or less. Since 0.225 is about the same as 0.22, these reproductive data do substantiate my observation that the population size has been constant over the years. Post et al. (1983) calculated a net reproductive rate of 2.72 for the increasing New York population. The authors also state that the net reproductive rate for the Cedar Key population was 1.11 (based on 1979-1980 data), but it is unclear how this figure was determined without life table (i.e. survivorship) data.

These New York and Florida projects are the only major long-term studies that report and summarize detailed reproductive data. Other papers that contain some data on breeding success and productivity for other subspecies of seaside sparrows are Nicholson (1946), Woolfenden (1956), Stimson (1956), Norris (1968), Sprunt (1968), Stimson (1968), Trost (1968), Woolfenden (1968), Worth (1972), and Werner (1975).

Territories and Territorial Behavior

Definition and Methods of Determining Territories

The working definition of "territory" I used in this study was "any defended area" (Noble 1939, p. 267). My use of the term "defended" implies that a bird exhibited aggressive behavior towards another, with the seeming intention of driving or keeping the other out of his or her territory. I considered vocalizations and visual displays directed at another bird to be defensive behaviors. This study dealt primarily with aspects of male territoriality, although female seaside sparrows also exhibited territorial behavior. I considered a territory to be an area in which a male invariably challenged intruders with singing, displays, or other overt aggressive behaviors.

All of my behavioral observations were made relative to the grid markers. I drew territory maps for the entire study population weekly, by connecting the points of the most peripheral singing perches with lines. I traced the territories thus delineated with a compensating polar planimeter and then calculated the enclosed areas. When a map indicated a boundary had moved by 15 m or more, I considered that to be a territorial boundary shift. The summary information regarding territory sizes and location reported in this chapter were those measured for non-experimental birds during the first week of May unless indicated otherwise.

Description of Territories at Cedar Key

Territories at Cedar Key were all purpose--used for mating, nesting, and feeding. Mated pairs exclusively occupied territories throughout the breeding season, although boundaries between territories fluctuated.

Only two instances of complete territory relocations were noted for 65 non-experimental males studied 1979-1982.

The mean yearly return rate for male territorial birds was 79% (N=89). There was a strongly significant tendency for males to re-establish territories on the same sites in succeeding years. (My conservative null hypothesis was: Returning males are as likely to establish a new territory as they are to re-establish their old territory. My sample sizes and statistics were: 43 re-established territories of 52 observed returnees; $\underline{X}^2$ one-sample test, $\underline{X}^2$=21, $\underline{df}$=1, $\underline{P}$<0.001). Year-to-year retention of territories has also been reported qualitatively in the few other studies of marked populations of seaside sparrows (Worth 1972; Werner 1975; Greenlaw pers. comm.).

The territory sizes of non-experimental birds at Cedar Key ranged from about 200 to 4000 m^2. The mean size was 1759 m^2 (SE=242 m^2, N=65). This average territory size for the population did not change significantly over the years 1982-1984 (Kruskal-Wallis one-way ANOVA, N=43 territories of non-experimental males, df=2, $\underline{H}$=0.83, $\underline{P}$>0.5). In comparing the individual males' territories from year to year, I found no significant increase or decrease in their territorial areas (Wilcoxon matched-pairs signed-ranks test, N=23, $\underline{T}$=91, $\underline{P}$>0.05).

The boundaries of territories did not follow any apparent natural landscape divisions, such as vegetation type borders or small tidal creeks. However, larger tidal creeks (>20 m wide) did often separate territories.

Territorial Behavior

Several studies of northern seaside sparrows (Post 1974; Post & Greenlaw 1975) contain a few quantitative data describing territorial

behavior. Other authors (e.g., Audubon 1831; Nicholson 1946; Norris 1968) anecdotally portrayed territorial and breeding behavior of seaside sparrows, some in detail and many from an anthropomorphic perspective. Those reports that best characterize territorial birds and their social interactions are Norris (1968), Worth (1972), and Werner (1975).

At Cedar Key males began to establish their territorial boundaries in early March by singing regularly from song perches, usually clumps of elevated vegetation such as Juncus tussocks located at the edges of their territories. Overt aggressive encounters were also first observed at this time and became most numerous in April. Behaviors of such encounters, in order of frequency of occurrence, were chasing bouts accompanied by strident "tchi," "zuck," and rapid "tuck" calls; supplanting (a challenger flew towards a perched bird, and the perched bird left without dispute); and short-range "facing off" displays, wherein the participants engaged in wing raises, bobbing, bill thrusting, and wing and tail flick displays, co-occurring with the "tuck" and "tchi" calls and "whisper songs."

These Early Season territory-establishment behaviors, as well as male-female pairing chases, decreased significantly in frequency and in duration as the breeding season progressed into May. By the end of the breeding season (June), territorial males seldom disputed intrusions by neighbors and floaters.

Prior to experiments I conducted in 1983-1984, Post and I believed that there were no excess males trying to establish territories and consequentially compress existing territory sizes. I found, however, that there were such males, as discussed below in Chapter IV.

Females definitely displayed aggressive behavior towards both intruding males and other females throughout the season, although I have few quantitative data on the extent of their involvement in territoriality. In contrast to males, which were more likely to give short distance aggressive displays and calls, females were more likely to supplant and chase intruders. Of the total 3,159 instances of overt aggressive behavior I analyzed between seaside sparrows in March and April, 22 percent involved females. Only 5 percent were known to be female-female encounters. Observations of such encounters were difficult to make, because females spent more time than males in dense vegetation. The frequency of female chases of intruders from the pairs's territory averaged 2.7 chases per hour in late March and early April. These chases were usually accompanied by the "tchi" vocalizations and sometimes by a fast rendition of the "whinny" vocalization (female solicitation call).

Reactions to Other Species of Birds and to Humans

I observed no vocal or other behavioral interactions of seaside sparrows with resident clapper rails or marsh wrens. Each of these species seemed oblivious to the sounds emitted by the others. Calls and songs often overlapped, even when given within close range (<15 m). This is in contrast to other studies of bird communities, in which singing characteristics of several species are influenced by each other (e.g. Popp et al. 1985). Several times I did note that seasides alternated songs in a definite pattern (countersang) with migrating red-winged blackbirds (Ageliaus phoeniceus) and bobolinks (Dolichonyx oryzivorus). Cruising fish crows (notable nest predators of seaside sparrows) almost always caused seasides to stop singing and sometimes to give "si

twitter" alarm calls (23 observations of low-flying fish crows during song, 18 instances of song ceasing).

Wintering sharptail sparrows incited aggressive behavior from seasides, especially when the sharptails began to sing in early May. The seaside's aggressive behavior was identical to that directed towards conspecific intruders. Early in the breeding season the mostly silent sharptails were tolerated and unchallenged. On 17 occasions I heard distinct countersinging between seasides and sharptails, although their songs are quite different.

My study population of seaside sparrows seemed oblivious to my presence, except when I approached to within 5 m or handled them. The birds were more wary when I was accompanied by field assistants. Other researchers have made similar observations regarding the "tameness" of their subject populations of seaside sparrows (Sprunt 1968; Post 1974). At Cedar Key curious sparrows and wrens approached within 1 m of me when I was still for 30 min or longer. Indeed, I once awoke from a nap on the ground to find a sparrow staring at me about 20 cm from my face!

My close approach to nests (<10m), however, did provoke alarm and sometimes distraction displays from the parents when they were in the nest vicinity. If the female was on the nest, she usually ran about 3 m then flew about 5 m farther away. Presumably these reactions are nearly the same as those given in response to other "predators." Several times I simulated identical predator-reaction behavior by placing a mounted fish crow model 2 m from a seaside nest. The typical response by the parents was high pitched "seeet calls" interspersed with the "tuck" call, given while the birds rapidly flitted around in the vegetation within 5 m of the nest. Three times I saw females give apparent

distraction displays by trailing their wings as they ran away from their nests.

Discussion of Seaside Sparrow Territoriality

Territory types and variation

The seaside sparrow literature indicates that different races, and populations within races (see Post 1974), may have functionally different types of territories. These have been described variously as colonies (Tompkins 1941; Sprunt 1968); areas with separately defended nesting and feeding areas (Woolfenden 1956, 1968; Worth 1972); grouped (defended) nesting territories with undefended remote foraging areas (Post 1974); nest-centered activity spaces ("Type B" of Wilson 1975; Post 1980); and all purpose breeding territories (mating, nesting, and feeding; "Type A" of Wilson 1975, Werner and Woolfenden 1983). The occasional references to seaside sparrows' being "colonial" may be misleading in that this designation implies the birds had very small territories, such as those of colonial shorebirds. Although the limited nesting habitat and the concomitant foraging behavior of some populations give the appearance of coloniality, seaside sparrow nesting groups are perhaps better described simply as aggregations.

I have reviewed the literature describing seaside sparrow habits and have observed populations from Florida to New York. I conclude that nearly all subspecies and populations exhibit the "all purpose" type of territoriality. A few populations (e.g. at Post's (1974) Gilgo Beach study site) exhibited variations of the all purpose type, in that the birds sometimes foraged out of their territories on undefended areas. Territories at Cedar Key were of the all purpose type. Occasionally

individuals were seen foraging, unchallenged, on other known
territories.

Territory quality and space use

Post and co-workers (Post 1974, 1981b; Post & Greenlaw 1982; Post et
al. 1983; Greenlaw & Post 1985) comparatively studied the
interrelationships of territory size and quality, predation, food
availability, reproductive success, and mating systems of seaside
sparrows on Long Island, New York, and at Cedar Key, Florida. Their
studies reached several conclusions with which I generally concur: Food
seemed not to be a limiting factor in determining territory size;
"Space-use patterns" (i.e. maintainence of territory size, and foraging
on and off the territories) were more influenced by the numbers of birds
attempting to settle into a habitable area than by food availability.

In other studies Post (1974) and Werner (1975) contended that it is
unlikely that territorial spacing limits the population size of seaside
sparrows. They suggested that as the density of birds increases over
the years the territory sizes simply decrease in order to accommodate
more birds. The population size at Cedar Key remained stable throughout
my study; thus, I did not have an opportunity to support or refute this
hypothesis under the circumstances of increasing population as described
by these authors. Territorial compression either did not occur at Cedar
Key, or if it did occur then the territories must have become maximally
compressed prior to my study. I conclude this after considering the
findings of my 1983 and 1984 experiments on territorial birds (Chapter
IV). Because I found that non-territorial males did exist, I contend
that territory boundaries and sizes are not necessarily so flexible as
to accomodate all aspiring breeders, as suggested by Post and Werner.

A few bird studies have established an inverse relationship between
territory size and resources (Zimmerman 1971; Seastedt and MacLean
1979). Greenlaw & Post (1985), however, found that the sizes of the
territories they investigated were not correlated with their composite
index of territory quality (which included nesting, food and
cover/protection factors). Furthermore, territory size was not directly
related to volume of vegetation, area of vegetation, or amount of food
on the territory (Post 1980).

Several recurrent conclusions appear in all seaside sparrow
literature describing territorial and feeding behaviors. My
observations on birds at Cedar Key support most of these: Territory
sizes and probably quality vary considerably within and among
populations. Food is seldom if ever a limiting resource, as
convincingly argued by Post et al. (1983). Animals with small
"nest-centered" territories simply forage, unchallenged, off their
territories. Both migratory and non-migratory males tend to establish
their territories in the same locations year after year. Territorial
shifts within a season rarely occur. Birds in dense populations spend
more time involved in aggressive behavior but neither spend less time
feeding nor suffer lower reproductive success as a result of crowding
(Post 1974). Male sparrows are probably not defending areas for the
food value per se, but are rather advertising and defending territories
in order to increase their chances of mating and keeping mates.

Extension of territory definition and function

Kaufmann (1983) stated that territoriality is one form of social
dominance, dominance being defined as priority of access to critical
resources (e.g. food, mates) that increase the fitness of the dominant

individual. Kaufmann further described territoriality as "relative dominance." Individual A may be dominant to a subordinate, B, while in A's territory, but not dominant to B when outside of A's territory. These interpretations of territoriality are more inclusive than the restricted working definition I gave at the beginning of this section. They synthesize that traditional, restricted definition of a territory as "any defended area" with the broader concept of social dominance. Kaufmann's characterization of territoriality as one manifestation of social dominance is quite applicable to seaside sparrows at Cedar Key. The territories were indeed vigorously defended areas, yet a male off his territory was invariably subordinate in another bird's territory. Males together on the few areas of the marsh not occupied by territories did not evidence dominant-subordinate behavior: apparently shared were food and the rare female affiliations that occurred outside of territories. Thus no dominance hierarchy or absolute dominance seemed to exist.

As Kaufmann (1963) pointed out, arguments about functions of territoriality have mostly been concerned with whether a territory serves as an area to enhance social stimulation, or as an area to allow resource acquisition. Evidence in support of the former hypothesis, proposed by Darling (1952), is that some birds clump their territories even when nearby suitable habitat is available. Considering the synchronized breeding behavior of seaside sparrows and the observation that populations do indeed clump their territories, one may concur that social stimulation is a function of territoriality in these birds. However, I do not believe this to be the case in the birds I have observed, for the following reasons.

First, I suggest that clumping is a response to many individuals having the same gestalt perception of preferred habitat, which researchers have not been able precisely to identify. Since food is apparently not limiting, I suspect that the preferred habitat for a male seaside sparrow selecting and setting up a territory is an area of the marsh that allows maximum singing display advertisement (i.e. moderately low vegetation with dispersed singing perches such as tussocks of Juncus). Singing and being able to be heard while singing are vital to the fitness of male seaside sparrows, as determined by experiments described in Chapter IV. Thus, what may initially appear to be suitable unoccupied habitat may in fact be unsatisfactory for establishing a song-defended territory. Secondly, I do not believe that social stimulation is a function of territoriality in seaside sparrows, because their apparently synchronized breeding behavior can almost always be directly attributed to weather and other environmental conditions, such as flooding.

For seaside sparrows at Cedar Key, the possession of a territory does seem unequivocally to allow the owner priority of access to the resources contained therein, the most important of these probably being singing perches, a mate, and a relatively undisturbed mating/nesting area. Thus the territories of seaside sparrows easily fit the conventional concept of bird territories' being "defended," areas exclusively occupied by a relatively dominant male. Also applicable is Kaufmann's broader characterization of a territory as "a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others which have priority elsewhere or at another time. This priority of access must be achieved

through social interaction" (Kaufmann 1983, p. 9). Because this definition includes temporal and relative dominance criteria, this definition more comprehensively characterizes seaside sparrow territoriality.

Introduction

Seaside sparrows (Ammodramus maritimus) have a vocal repertoire of distinctive calls and song types. Because these birds are cryptic and tend to remain low in their densely-vegetated salt marsh habitat, vocal communication is important in their social behavior. Intergradations and varying contextual uses of sounds presumably convey different information to other birds receiving the messages.

Most older seaside sparrow literature is descriptive, and vocalizations are reported in general and anecdotal behavioral observations (Kopman 1915; Sprunt 1924; Holt & Sutton 1926; Howell 1932; Stone 1937; Tomkins 1941; Nicholson 1946; Woolfenden 1956; Norris 1968; Trost 1963; Worth 1972; Lowery 1974). Relatively recent studies of the northern seaside sparrow (A. m. maritimus) by Post & Greenlaw (1975) and of the Cape Sable seaside sparrow (A. m. mirabilis) by Werner & Woolfenden (1983) include more objective descriptions of calls as well as songs and associated behaviors. Post & Greenlaw's (1975) detailed description of the vocal and display repertoire of their Long Island, New York, population is especially thorough.

In this chapter I describe and discuss the vocalizations of a Florida population of Scott's seaside sparrow, A. m. peninsuale. I include more quantitative and conclusive data than in my preliminary report on Scott's seaside sparrow vocalizations (McDonald 1983c). This

chapter also compares the vocalizations of my study population to those of northern seaside sparrows described by Post & Greenlaw (1975) and to those of Cape Sable seaside sparrows described by Werner & Woolfenden (1983).

General Methods of Data Collection and Analysis

The project history, study site, and subjects were described in Chapter II.

Coverage

I recorded vocalizations and described the behavior of the study population throughout the years 1981-1984. My most intensive field work occurred during the breeding seasons (late February through mid-June) when I went to the marsh at least 3 days/week. I also visited the marsh about once every 10 days during the remainder of the year. During the breeding season I made the majority of my behavioral observations and recordings when the birds were most active--from just before sunrise until about four hours after sunrise. The birds' activity level increased again moderately about an hour before sunset. The few evening behaviors and vocalizations I recorded seemed not to differ from early morning observations, thus I only mention their occurrence in this chapter. Unless otherwise noted, my quantitative descriptions of vocalizations and behaviors are for observations taken on mild spring mornings when the temperature ranged from $18-33^{o}$ C, there was no precipitation, and the wind ranged from 0-24 km/h.

Sample Size and General Observation Methods

The total number of marked birds (1981-1984) was 213, including birds manipulated in 1983-1984. In generalizing about the use of vocalizations, I considered only data for 91 mated and 11 unmated birds that I had observed for at least 15 h per season. Detailed analyses were based on fewer males, as described below. I studied each subject male at least one hour per week throughout the breeding season. On a typical morning I observed 1-3 focal males for about an hour (an hour's "time budget" block), then watched another 1-3 males for the next hour, and so on up until about 0900. I randomly determined the sequence of these time budget observation blocks. Thus, all birds received approximately equal coverage that was representative of the morning hours. Females were difficult to observe; I described their behaviors and vocalizations as parts of their mates' time budgets.

During the time budget I dictated all observed behaviors and the birds' locations on cassette tape. I made most recordings (including all used for sound analyses and sonograms in this section) with a Sony TC 150 cassette tape recorder (Mineroff-modified), using a Bell and Howell "Shotgun" unidirectional electret condenser microphone with windscreen. I measured the amplitude (in dB) of a singing male 7 m from me with a Bruel & Kjaer Sound Level Meter (Type 2219) on 5 Apr 1985.

I also used field data forms to record contextual information, banding records, nest descriptions, territorial boundaries, and other biological information. Territory maps for the entire population were drawn in the field at least bi-weekly throughout the breeding seasons.

General Analysis of Notes and Recordings

I transcribed, tabulated, and summarized the behavioral data. I determined characteristics of tape recorded sounds (e.g. frequency ranges, length of song) with a Uniscan II FFT Real Time Sonogram Spectral Display (Model 4600), and prepared sonograms (Fig. III-1 through Fig. III-10) with a Kay Elemetric 7029A Sono-graph using the wide-band filter (300 Hz) and either the 80-8000 Hz or the 1600-16,000 Hz scale. The specific vocalizations and behaviors I analyzed are listed in Table III-1.

Detailed quantitative descriptions of vocalizations and other behaviors were determined from an analysis of 103 time budget hours of 30 mated and territorial best-studied males. I chose time budgets for analysis based on comparability of day of year (Apr-May), time of day (sunrise-0900), and the typical mild weather conditions described above. I used non-parametric statistics (Siegel 1956; Conover 1980) for the analyses.

My specific methods of investigating flight songs ("complex flight vocalizations" of Post & Greenlaw 1975) and countersinging are discussed in separate sections below.

Table III-1. Vocalizations and behaviors measured during time budget
observations (in min and sec duration, and frequency)

Singing[a,b]
    Primary song
    Whispering song
    Matched countersinging
    Not matched countersinging
    Flight song

Other Vocalizations[a,b]
    Tuck
    Tsip
    Si Twitter
    Seeep
    Tchi
    Tchi flight
    Whinny
    Zuck and other calls

Position Changes[a,b]
    When not singing
    Singing, song type change
    Singing, no song type change
    Singing, stop singing

Observations Relating to Females and Young[a,b]
    Female present
    Female solicitation calls, other calls
    Copulations
    Females building nests
    Other behaviors related to females and young

Other Behavior[a,b]
    Feeding, resting, and preening
    Off territory: feeding; invading nearby territory

Reactions to Intruders[a,b]
    Frequency, duration, and location of intruder
    Flight chases
    Vocalizations: Displays:
      Solo primary song   Sham-preen
      Countersong   Grass-pick
      Whispering song   Bob and bill jab
      Calls (as above)   Contact

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[a]Contextual information also noted: bird's identity, location, mated
status; presence of conspecifics, date, weather, and location of
observer.

[b]Terminology follows Post & Greenlaw 1975.

Results and Discussion of Calls and Song

Descriptions and Use of Vocalizations

Scott's seaside sparrows make 14 distinct vocalizations: a primary song, three modifications of the primary song, and 10 calls. The probable functions of their songs and calls are summarized in Table III-2. I distinguish "songs" from "calls" as implicitly defined by most ornithologists, and as specifically stated in Pettingill's working definition: "Song is a vocal display in which one or more sounds are consistently repeated in a specific pattern. It is produced mainly by males, usually during the breeding season. All other bird vocalizations are collectively termed call notes or, simply, calls" (Pettingill 1970, p. 319). I use Post & Greenlaw's (1975) vocalization terminology throughout, except for "whispering primary song," which is from Werner & Woolfenden (1983).

Table III-2. Vocalizations of Scott's seaside sparrows

Vocalization Name[a]	Sex and Context[b]	Probable Function(s)
Primary song	Male; 1, 2, 4	Territory defense and mate attraction
Whispering song	Male; 1	Territory defense during intrusion
Complex flight vocalization	Male; 1, 2, 5	Territory defense and mate attraction
Subsong (young birds)	Male; 1, 4	Practice song
Tuck	Male and Female; 1-5	General purpose; moderate aggression; chase; nest defense
Tsip call and Si twitter	Male and Female; 1-3, 5	Heightened aggression; attack; nest defense
Seeep note	Male and Female; 1, 2, 5	Proclaim location of female(?); fear(?); Flocking (fall & winter)
Tchi vocalization	Male and Female; 1-3, 5	Moderate aggression; chase; female: nest area distraction, proclaim sex
Whinny vocalization	Female; 1, 2, 4	Attract males for copulation
Zuck call	Male and Female; 1, 5	Heightened aggression; chase; drive off young
Scree call	Male and Female; 3	Extreme distress call
Begging and Chup calls	(given by young only)	Begging for food

[a] Terminology follows Post & Greenlaw (1975). This table is modified from Post & Greenlaw's (1975) Table 3, which summarized "vocal displays" of northern seaside sparrows.

[b] Contexts in which the vocalization were elicited: 1-in presence of intruder or neighbor bird; 2-in presence of mate; 3-in presence of predator, or human disturbance; 4-also given when bird apparently alone; 5-given in flight.

Calls of Scott's seaside sparrows

In this section I give sonograms, descriptions, and suggested functions of 10 calls, presented in approximate order of their frequency of occurrence during the breeding season.

Tuck call

The "tuck" (Fig. III-1A) was the most common of the calls. It was given by males and females throughout the year. The short tuck covers a wide frequency range and is probably the same call Werner & Woolfenden (1983) labeled as the "chip" call for Cape Sable seaside sparrows. The tuck appeared to be an all-purpose vocalization, but seemed to function mostly as a general alarm and moderately intense aggressive call. It was invariably given during short-distance aggressive interactions and usually accompanied by wing and tail flicks, and by the "tsip" calls (shown specifically in Fig. III-1A).

Males gave tuck calls at an average rate of 0.3 min/h when there was no apparent disturbance on their territories. During intrusions, however, the tuck rate increased to 13.5 min tucking/h intruder present. This call was also given alone (or together with "tsips") by both parents when a predator or human approached a nest within 5 m. The tuck call was the only one I heard regularly during the non-breeding season. I also heard fledglings and juvenile birds give this call.

Tsip and si twitter

Both males and females also gave the higher-pitched, short "tsip" call (Fig. III-1B). When birds were highly agitated the "tsip" was rapidly repeated, thus intergrading into the "si twitter" call. The "tsip" was often interspersed with "tuck" calls, as mentioned above, and

was accompanied by wing and tail flicks. During bouts of calling, which lasted 0.25 to 17.3 min, birds gave "tucks," "tsips," and combined "tuck-tsips" at a rapid and usually regular rate of 30-145 calls/min. As with the "tuck" call, "tsips" and "si twitters" generally signaled alarm and aggression, but more often indicated a higher level of alarm. My closest approach to nests (<2 m) and my placing of a stuffed fish crow near nests nearly always elicited "si twitters." I never heard "tsips" or "si twitters" from undisturbed birds. During intrusions the average combined "tsip-si twitter" rate was 4.5 min tsip-si twitters/h intruder present. I only rarely heard the "tsip" call during the non-breeding season, and I never heard fledglings or juveniles give either of these calls.

Seeep note

During the breeding season I occasionally heard females give a soft, high-pitched "seeep" call Fig. III-1C). Most of the "seeeps" occurred during bouts of copulation. Sometimes a female gave this call as a nearby male began to sing relatively softly (Fig. III-2A). Post & Greenlaw (1975) suggest that the "seeep" call conveys a weak fear message. This call, or a very similar one, was the second most common vocalization I heard outside of the breeding season. Males and females of both Scott's seaside sparrows and wintering sharptail sparrows at Cedar Key gave "seeeps," especially in the late fall and early winter. I agree with Post & Greenlaw (1975), and with Werner & Woolfenden (1983), that this call probably functions as a social and flocking vocalization outside of the breeding season.

Tchi vocalization

The loud and relatively short "tchi" call (Fig. III-2B) was given by both sexes and was most often heard during chases. About half of the total "tchis" I heard were given during or immediately following chases. Usually the "tchis" were rapidly repeated, and frequently they intergraded with a slower, slurred "tyu." The "tyu" itself often slurred into a "whinny"-like vocalization (described below). The "tchi" call was probably the same as the "squeaz" call described by Werner & Woolfenden (1983), and the same as the "jee-jee-jee-jee-jee-jeeeu-jeeeu" call described by Norris (1968).

The primary function of this call seemed to be signalling general aggression during chases. Frequently, however, I heard females give rapid "tchis" in flight ("tchi flight") as they left a nest they were building or incubating, even though no threatening bird seemed to be in the vicinity. These nest-departure "tchis" were not given adjacent to the nest, but rather at about 10-15 m from the nest. During a 1 h observation of nest building in early May 1983, for example, I saw a female depart and come into her nest 18 times. Fifteen of her departures were accompanied by "tchis," but only one arrival was accompanied by this call. Jon Greenlaw (pers. comm.) reports that female northern seaside sparrows behave in a similar manner. I suggest, therefore, that the "tchi" also functioned as a distraction call by drawing a potential predator's attention away from the nest as a female departs. Jon Greenlaw (pers. comm.) also thinks that "tchis" in the nest vicinity function to let the resident male know that this departing and arriving bird is a female who belongs, rather than an invading male.

Other than the females giving the "tchi" as described above, I seldom heard this call when no intruders were present (0.11 male tchis/non-intrusion hour). It was difficult to quantify the "tchi" rate during intrusions. On the average, however, a territory owner spent 2.62 min chasing/h intruder present. I estimate that at least half of these chases were accompanied by rapidly repeated "tchis," most of these calls given by the owner.

Whinny vocalization

I heard only females give the "whinny," with one unusual exception described below. This whirling, quavering call varies in rate from 0.3 to 3/sec (Fig. III-3). The whinny was the female's solicitation call; it functioned to attract a male. Females gave this call more often when a male was relatively close to her (within about 7 m), and especially if the male was singing. Males were immediately attracted to the "whinny" vocalization, and copulation usually followed. Even though females gave the "whinny" from on or near the ground, males seemed to have had no problem finding the vocalizing females. It is likely that some auditory characteristic(s) of this vocalization made it easy to locate.

Females gave this call most often prior to, and during nest building. Because females usually initiated up to 5 clutches per breeding season, the overall intensity of "whinnies" heard for the population remained the same from late March through May. The average whinny rate heard on all territories during these months was 2.02 min whinnies/h.

Post & Greenlaw (1975) describe the postures associated with the "whinny" vocalization and copulation. Werner & Woolfenden (1983) do not describe a female solicitation vocalization.

I only once heard a male give a distinct "whinny" (as opposed to the "whinny"-like "tyu," described above). On 6 May 1984 a male invading an experimentally muted bird's territory repeatedly gave whinnies while he intruded.

Zuck call

The loud, raspy "zuck" (Fig. III-4) was an aggressive call given during intense fights. Most of the zucks I heard were given by males, but sometimes females and juveniles gave this call. It may have been the same as the "Shu-shu...shu" call of Cape Sable seaside sparrows that Werner & Woolfenden (1983) mention but do not describe. In addition to its functioning as a general, high intensity aggressive call, "zucks" were the vocalizations most often given by fathers when they drove their older, almost independent fledglings off their territories (about 2-3 weeks post-fledging). Other than these father-fledgling encounters, I never heard this call given during non-intrusion circumstances. During intrusions both territory owners and intruders gave "zucks" (often mixed with "tchis") at the rate of 0.7 min zuck/h intrusion.

Other calls

The "Scree" (Fig. III-5) was a harsh distress call I heard only (with a few rare exceptions) from a few birds trapped in mist nets and being handled. Both sexes of adults and juveniles gave this call.

The monotonous and insistent "Begging Calls" (Fig. III-6), given by older nestlings and fledglings, were heard most often towards the end of the breeding season. Nestlings gave "Peep" (Werner & Woolfenden 1983) and "Chup" (Post & Greenlaw 1975) calls.

Post & Greenlaw (1975) describe one further call I have not mentioned--the "Chew" call. To my knowledge, I never heard this call at

Cedar Key. Jon Greenlaw (pers. comm.) proposes that the "Chew" call is probably a modified "tchi-whinny" vocalization.

Figure III-1. (A) Audiospectrogram of Tuck call (short notes around 8 kHz), and 1 interspersed Tsip call (vertical note). (B) Audiospectrogram of Tsip call. (C) Audiospectrogram of Seeep note.

A

B

C

16

12

8

kHz

0

0.5

1

0

TIME IN SECONDS
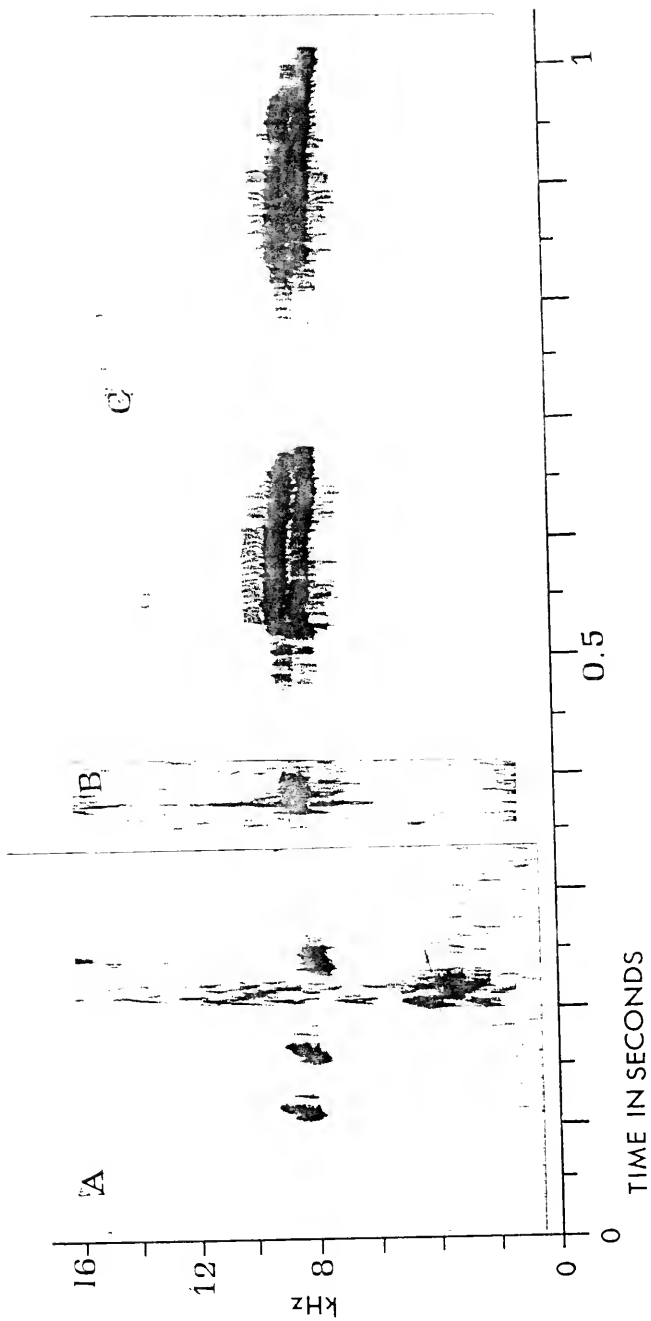
Figure III-2. (A) Audiospectrogram of Male Primary song and concurrent female Seeep note (indicated with "X"). (B) Audiospectrogram of Tchi call.

A

B

TIME IN SECONDS
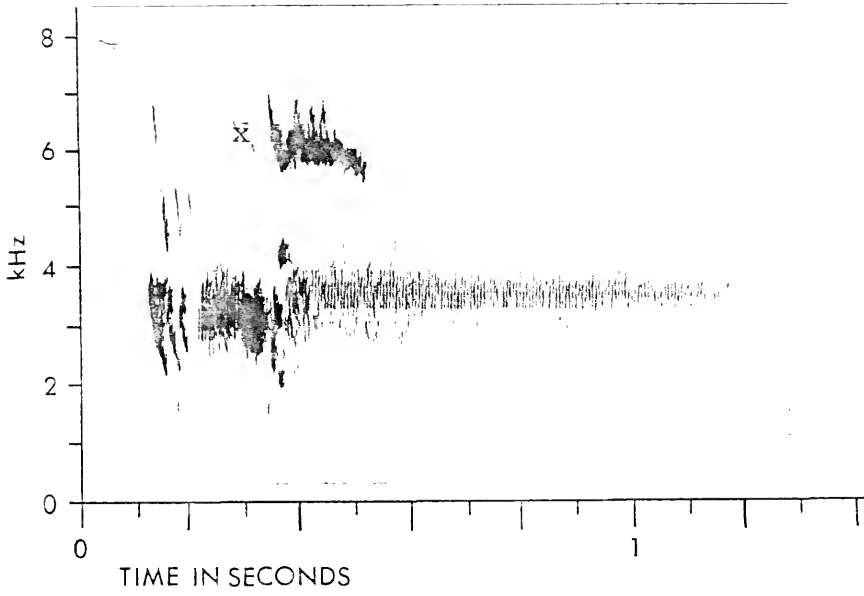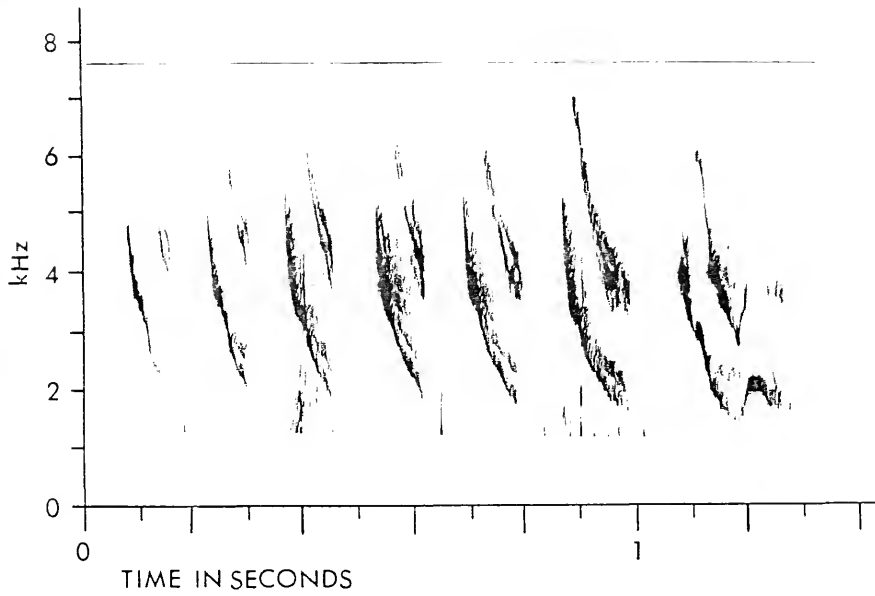
Figure III-3. Audiospectrogram of Whinny vocalization.

kHz

TIME IN SECONDS
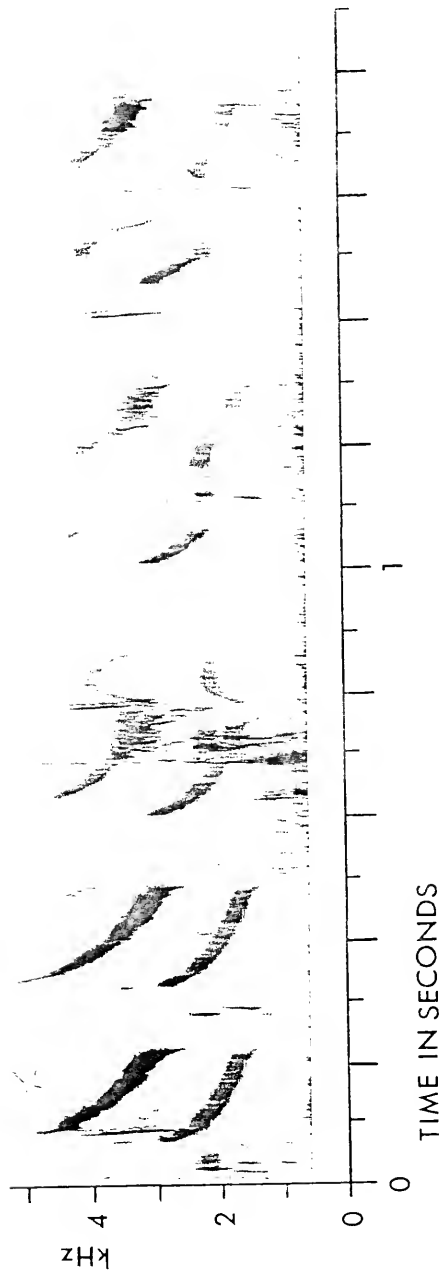
Figure III-4. Audiospectrogram of Zuck calls.

kHz

TIME IN SECONDS
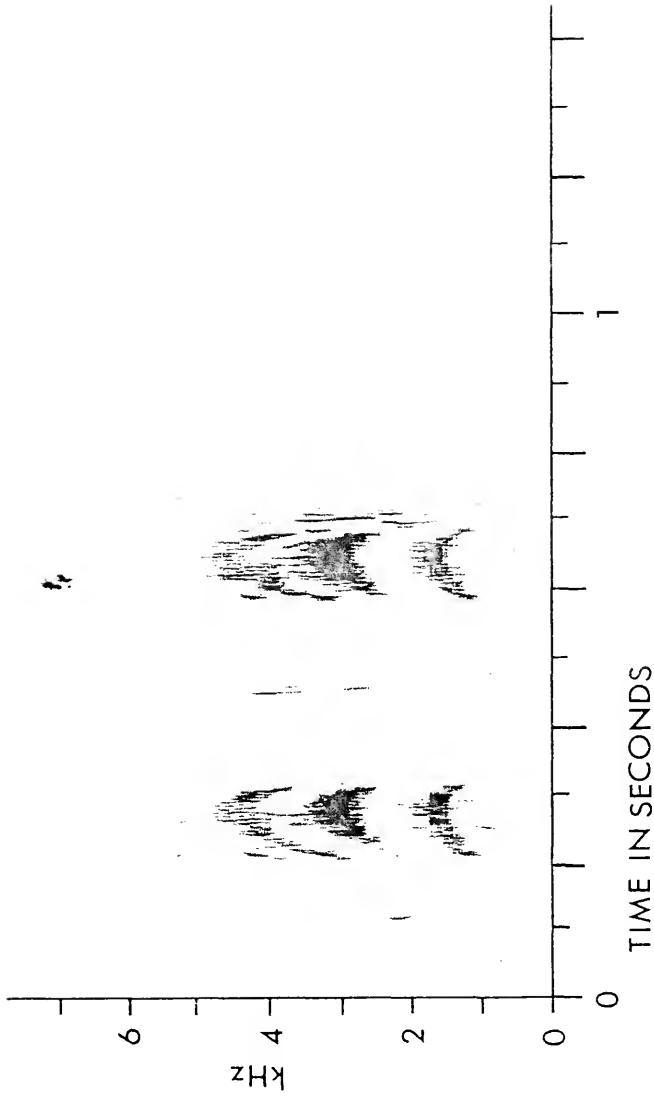
Figure III-5.   Audiospectrogram of Scree calls.

kHz

TIME IN SECONDS
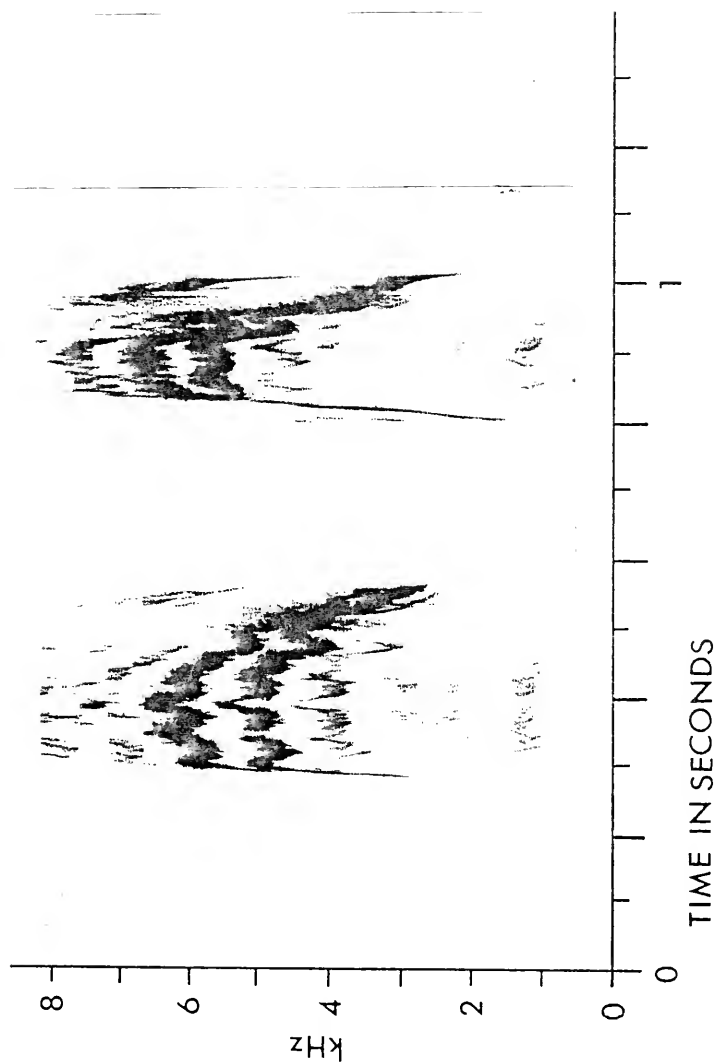
Figure III-6. Audiospectrogram of Begging calls from two nestlings, individuals A and B.
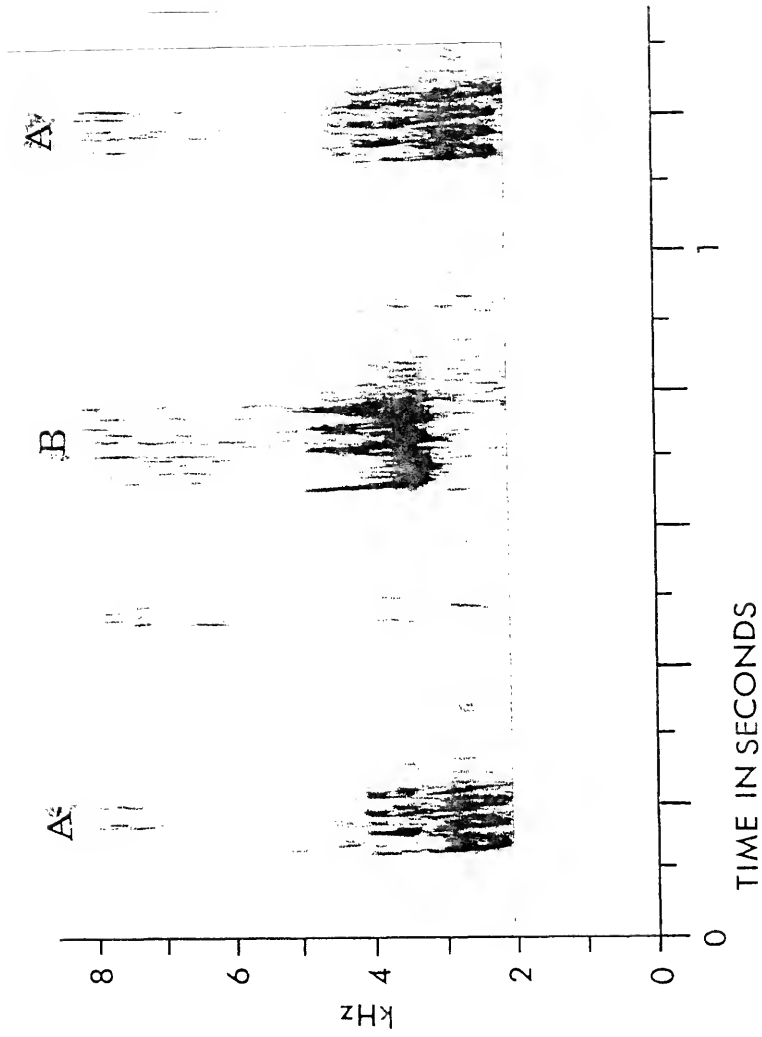
Figure III-7. Audiospectrogram of Primary song.

kHz

TIME IN SECONDS
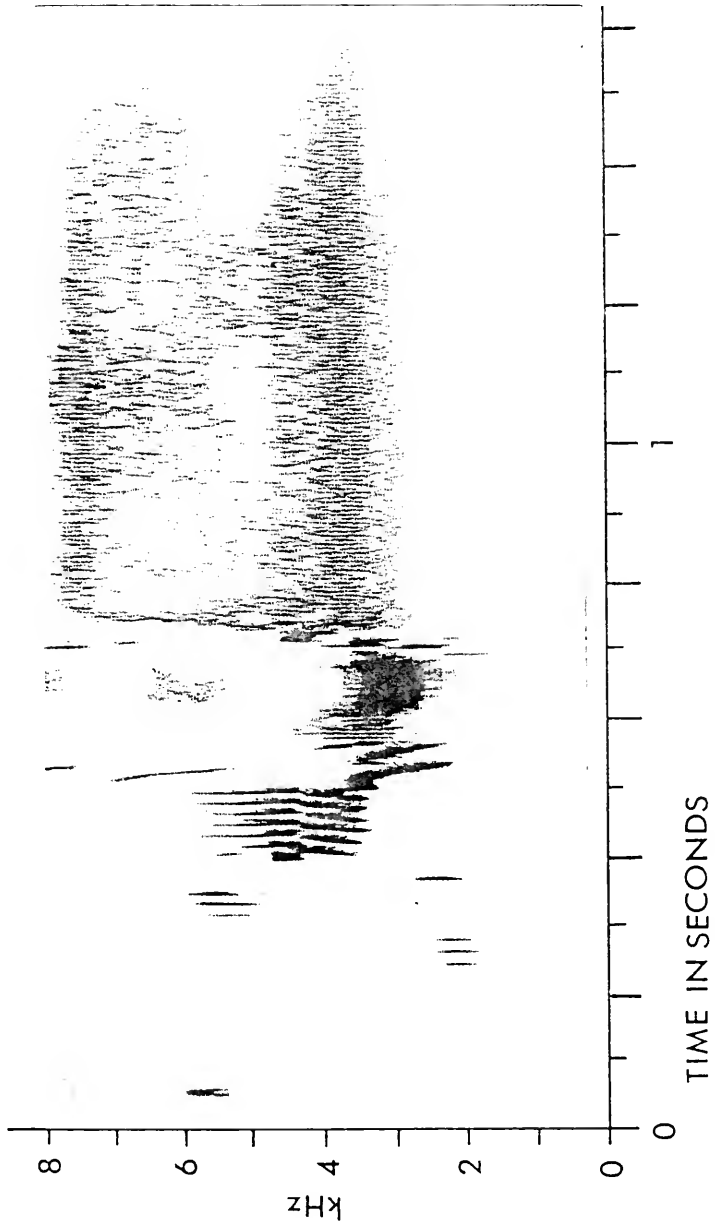
Figure III-8. Audiospectrogram of Subsong.

kHz

TIME IN SECONDS
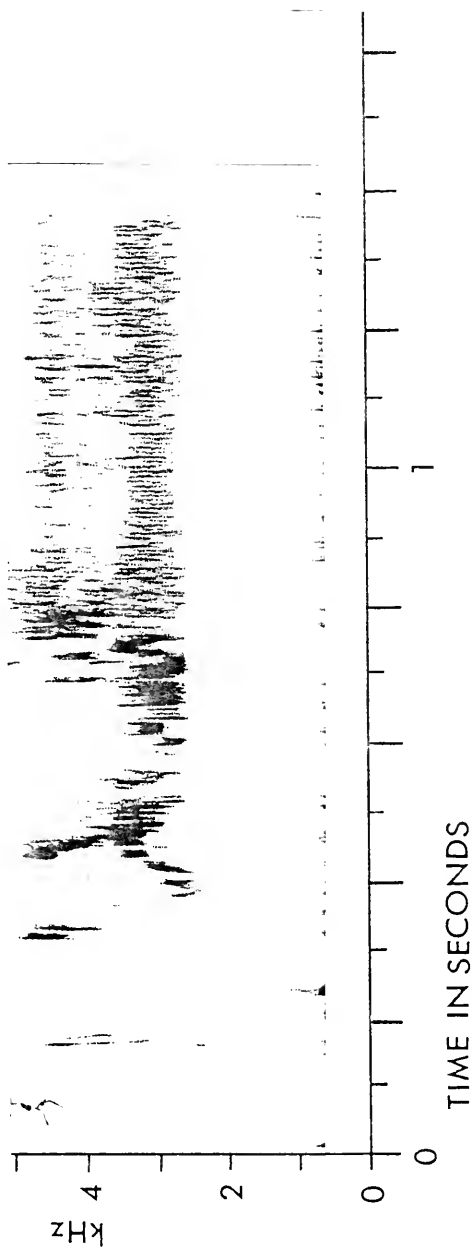
Figure III-9. Audiospectrograms of Countersinging from two males, individuals A and B.

A

kHz

TIME IN SECONDS

B

kHz

TIME IN SECONDS
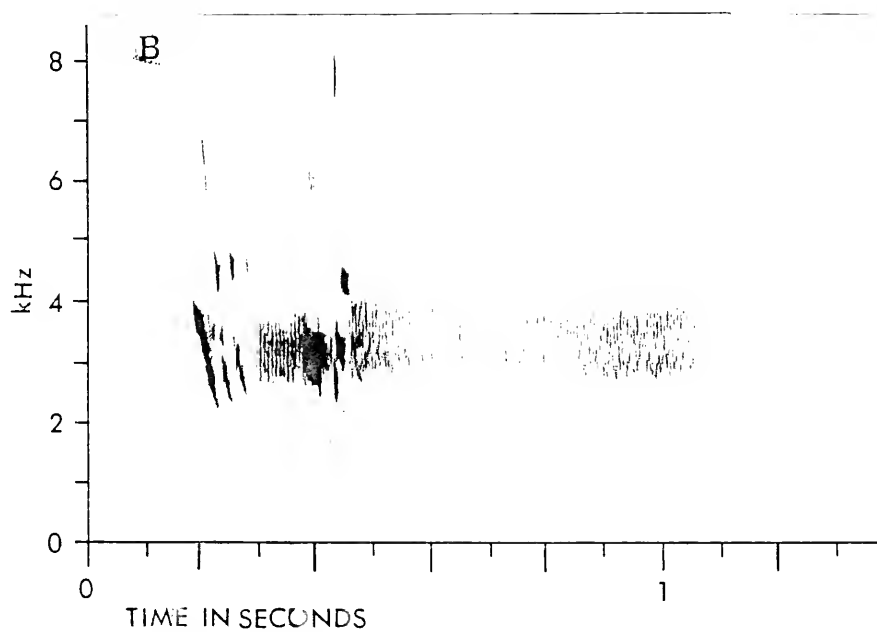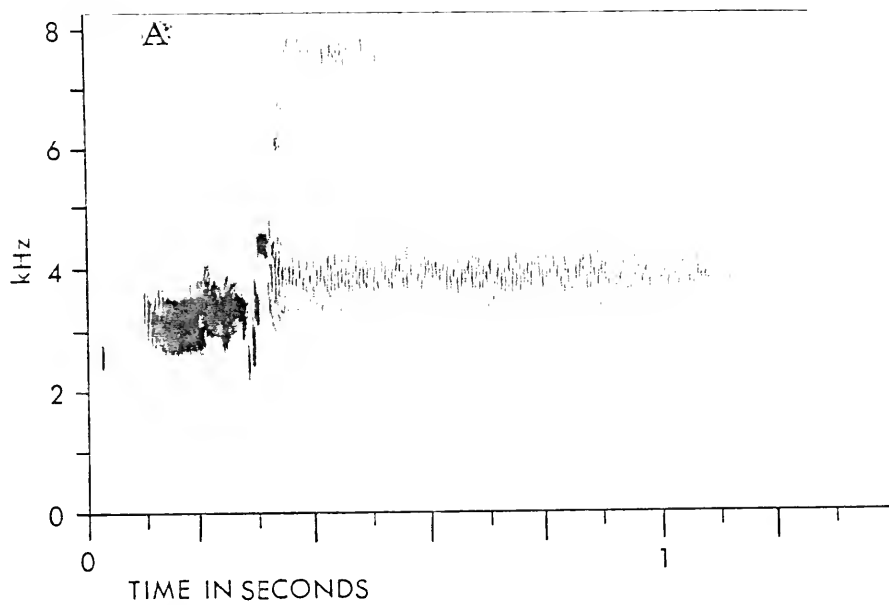
Figure III-10. Audiospectrogram of Flight song.

TIME IN SECONDS

kHz
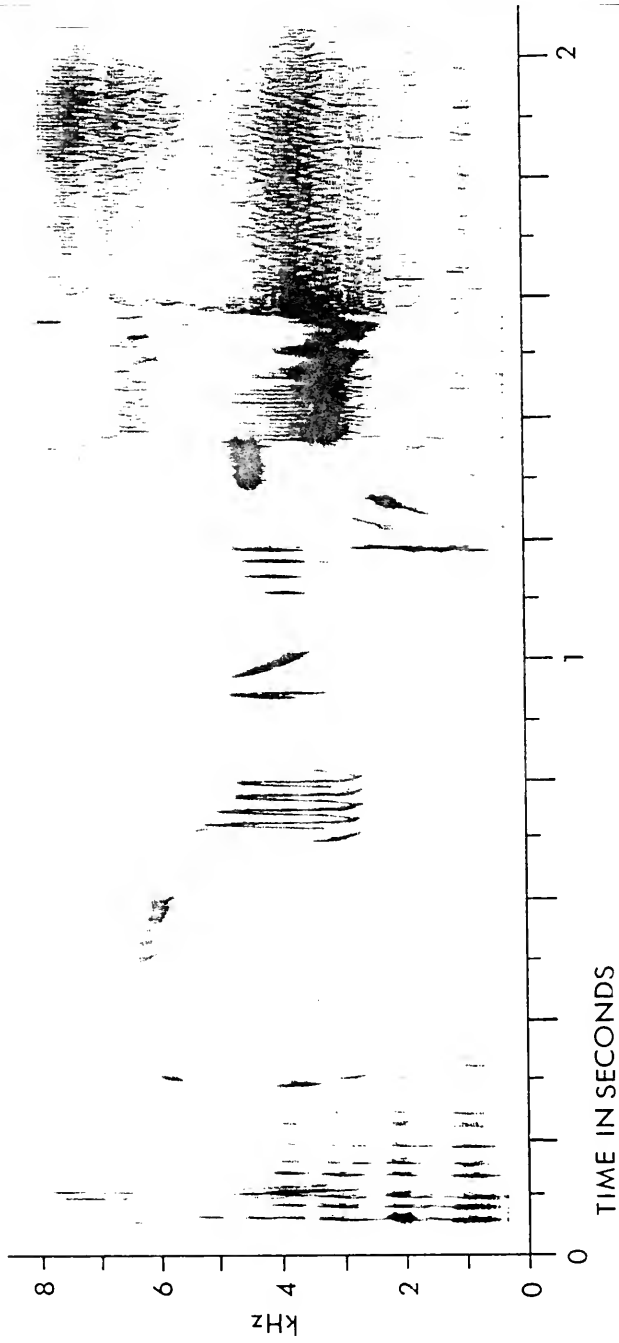
Primary song

Audiospectrogram. The seaside sparrow primary song (Fig. III-7) is relatively simple. The introductory portion of rapid clicks (centering around 6.5 kHz) is immediately followed by a buzzy trill (centered around 3.3 kHz). These frequency ranges and the song duration of about 1.0 second were characteristic for the entire population.

General description of singing behavior. During my study, only males sang. Although Post & Greenlaw (1975) describe "female songlike vocalization" that resembles male song, I never heard a vocalization of this type at Cedar Key. Males sang to delineate territories and to attract females. Experimental evidence for these functions of song is given in Chapter IV.

Males usually sang from elevated perches, such as tussocks of Juncus. Most birds had 3-7 favorite singing perches within their territories from which they gave about 85% of their songs. From 1979-1984 only two males sang from grid marker stakes, although Post & Greenlaw (pers. comm.) found that birds in their dense study population often sang from grid markers.

The singing pattern of seaside sparrows is similar to that of many song birds (Table III-3). Birds sang in "discontinuous" patterns of song "bouts" (songs repeated continuously without a pause), of "eventual variety" (song type change after three or more repetitions of the same song type) (Hartshorne 1956; 1973). An average bout throughout the season consisted of 19.2 songs and lasted 1-5 min (mean = 1.62). Highly variable periods of silence (mean = 7.9 min) separated song bouts. Males changed perches during 17% of these between-bout silences, before resuming singing. Song rate within a bout ranged from 6-9 songs/min

Table III-3. Characteristics of solo primary singing and countersinging of 30 mated male Scott's seaside sparrows during April and May

Characteristic[a]	Primary Song (Solo) Total	Countersong Total	Matched[b]	Not Matched[b]
N (bouts)	391	223	143	30
Mean bouts/h obs.	3.80	2.17	1.39	0.73
Total min sing	635	631	438	192
Mean min sing/h obs.	6.16	6.13	4.26	1.86
Mean min song/bout	1.62	2.33	3.07	2.40
Total bouts edge[c]	198	123	30	43
Total bouts center[d]	117	41	26	15
Total min edge	315	369	275	94
Total min center	193	110	66	44
Mean song type switches/bout	<0.01	0.02	0.02	<0.01
Mean song type switches/h sing	0.32	0.33	0.47	0.29
Mean perch changes/h sing	0.97	0.33	0.31	0.35
Mean perch changes/ bout	0.16	0.02	0.02	0.01
Mean perch changes/ bout with song switch	<0.01	<0.01	<0.01	<0.01
Mean perch changes/ bout without switch	0.03	0.02	0.02	0.01
Mean perch changes/ bout, song cessation	0.13	0.05	0.01	0.02

Table III-3, continued.

[a]Characteristics of solo primary singing and countersinging determined from analyses of 103 h of time budget observations, when no intruders were present on focal birds' territories. Other conditions during time budget observations are described in the text.

[b]Rate values calculated for Matched and Not Matched columns based on number of bouts and minutes of Matched and Not Matched singing, respectively. Thus the sums of rates of Matched and Not Matched values do not add up to the Total column for Countersong.

[c]Edge defined as the outer-most 10 m of the bird's territory.

[d]Center defined as the area within a 25 m radius of the estimated center of the bird's territory.

(mean = 7.7), close to the 6.6 song rate Woolfenden (1956) reported for New Jersey birds, and slightly lower than the 10.6 song rate reported by Post & Greenlaw (1975).

Individual males had a repertoire of two to four similar song types (mean = 2.41). When both solo singing and countersinging, birds seldom switched song types within or even between song bouts. The mean rate of song type switches during a bout was about 0.01/bout. Thus their singing was extremely "monotonous," sensu Hartshorne (1956; 1973), because their singing pattern was both continuous and of low "versatility" (infrequent song type changes).

Most males shared their song types with nearby territorial birds. A few of the birds had one highly distinctive song type within their repertoire that enabled me to recognize individuals aurally from as far away as 150 m. I did not detect any tendency for males to have a preferred song type from within their small song repertoire.

Seaside sparrows at Cedar Key seldom began a new song type after moving to a new perch while singing (Table III-3). Of a total 67 incidents of perch changes during singing, there was only one concurrent song type change. This constrasts with Krebs's (1977a, 1978) "Beau Geste hypothesis" that territorial birds switch song types when changing perches, thus possibly giving potential intruders the impression that territories are saturated.

Influence of abiotic factors on singing behavior. Singing activity varied throughout the year. It was most intense relatively early in the breeding season (late March through mid-April), especially before and just after birds were mated. The average time singing of 29 males measured 1-15 Apr 1983 was 19.4 min singing/h. In the third week of May

their song rate decreased to 12.1 min singing/h, a significant

difference (two-tailed Wilcoxon matched-pairs signed-ranks test, $\underline{T}=2$,

$\underline{P}<0.01$).

Weather modified the intensity of singing, on both a daily as well

as a seasonal basis. Very early in the spring (February through mid

March) birds sang more as the day warmed slightly, up to about 20° C.

During the middle and especially towards the end of the breeding season,

birds sang less as the day warmed. Virtually all singing stopped at

temperatures above 32° C, regardless of the time of day. From the middle

of the breeding season till the end, birds sang more on cloudy, cool

mornings. Light rain also enhanced singing activity at this time of the

year, and even heavy rain and thunder and lightning dampened singing

activity only slightly. Brisk winds (>25 km/h), however, greatly

reduced singing activity, especially early in the season on cool days.

The intensity of singing activity also varied throughout the day.

Peak song activity was early in the morning, from sunrise to about 3

hours after sunrise. The earliest I heard singing was 20 min before

sunrise. Birds also sang in late afternoon until about one-half hour

after sunset. Compared to seaside sparrows on Long Island, New York,

that I observed in June 1982, birds at Cedar Key sang less in the

evenings. The first morning and last evening songs were similar to

songs given during peak morning activity, except the song rate

(song/min) within the bout was lower very early and late in the day.

Influence of other birds on singing behavior. Unmated males sang

significantly more bouts than mated males, and thus their total time

singing (21.4 min/h) was greater than that of mated males (12.3 min/h),

as measured in May (two-tailed Mann-Whitney $\underline{U}$-test, N=30 and 11,

$P<0.01$). Singing rate also differed significantly according to whether an intruding male seaside sparrow was present. After territories were well established (by mid-April), intrusions were rare (mean = 0.7 min intrusion/hour). When an intrusion did occur an owner's first reaction was increased singing, and this was often successful in repelling the intruder. If the intruder was not driven off by normal primary song, territory owners switched to short-distance and more aggressive vocalizations and behaviors--whispering primary songs, tuck and si twitter calls, chases, quivering wing raises, and (rarely) contact fights.

The "whispering primary song" (Werner & Woolfenden 1983) was a slowly delivered (mean=3.5 song/min), low amplitude, and slightly lower pitched modified primary song. It was usually given by a male perched near the ground and confronting an intruder at 1-5 m. The whispering primary song was delivered with an almost closed beak, in contrast to the normal primary song where the bird threw back his head and opened his beak wide as he sang. I do not have data describing reactions of males that heard these whispering songs. Because I only heard it during agonistic encounters, this vocalization may have functioned to transmit a message of threat and liklihood of attack. Jarvi et al. (1980) described a similar use of modified primary song in the willow warbler (Phylloscopus trochilus) that transmitted a message that the singer was likely to attack his opponent.

Because short-distance encounters were more often accompanied by calls and displays, the combined normal and whispering primary song rate during intrusions (2.4 min song/h intrusion) was much lower than the song rate when no intruder was present (12.3 min song/h non-intrusion).

Calls of most other marsh birds, including the raucous clapper rails, seemingly had no effect on the seaside sparrows' vocalizations or other behaviors. Seaside sparrows did respond antagonistically toward vocalizing sharp-tailed sparrows (Ammodramus c. caudacuta) when these wintering migratory birds began singing prior to their departure the first week in May.

Subsong

Young males sang rudimentary subsong late in July and in August (Fig. III-8). These songs consisted of garbled warbles and parts (usually the terminal trill) of the adult primary song. Subsong was not as loud as the primary song and was sung only sporadically instead of in bouts. These first song attempts improved and came to resemble the adult's primary song by late fall, when virtually all singing activity stopped. Both yearling and adult males began to sing again in late February, and songs of the first year birds could still be differentiated from those of older birds. By mid-March, however, songs given by first-year and older birds could no longer be distinguished.

Countersinging and Repertoire Use

Introduction and comments

Countersinging occurs when two, three, and sometimes four male birds alternate their songs in a regular pattern. Countersinging is described as "matched" when the same song type or types are sung by the participating birds. The behavioral and evolutionary significance of song repertoire sharing in general, and of song matching during countersinging in particular, has been the subject of recent stimulating studies (Krebs & Kroodsma 1980; McGregor et al. 1981; Payne 1982; Kramer et al. 1985; Searcy et al. 1985).

Many relatively simple explanations for song matching exist:
Matching indicates high-intensity interactions (Lemon 1968b). Birds
match in order to monitor the positions of their neighbors (Lemon
1968a). Relative dominance between countersinging birds influences the
degree of matching (Kroodsma 1979). Time intervals between songs of
countersinging birds indicate which of the participants is dominant
(Smith & Norman 1979). Matching functions as a vocal threat that
regulates distance between birds (Todt 1931). Matching is a graded
signal used in territorial encounters (Krebs et al. 1981). Finally,
matching indicates readiness to interact aggressively (Horn & Falls
1986).

Further interpretations of song sharing that deal more generally
with repertoires and repertoire sharing (which may or may not involve
matched countersinging) are: Larger song repertoires make recognition
of neighbors more difficult (Falls & d'Agincourt 1981; Searcy et al.
1981). Larger repertoires are more attractive and stimulating to
females (Howard 1974; Searcy et al. 1982). Larger repertoires allow
resident birds to fool potential intruders through increasing the
perceived density of singing birds (Krebs 1976), and, young indigo
buntings (Passerina cyanea) mimic the repertoires of older territorial
males and thus deceive other males through mistaken identity (Payne
1982). Searcy et al. (1985) found no correlation between song repertoire
size and male "quality" in song sparrows (Melospiza melodia).

While these may or may not be adequate explanations for song sharing
in birds, some recent experiments on song sharing have become
increasingly sophisticated. These studies have incorporated more
objective methods of determining song similarity, the possible effect of

sound degradation from sender to receiver influencing behavior, the birds' natural use of their repertoire, and their familiarity with neighboring males (Falls et al. 1982; Schroeder & Wiley 1983b; Whitney & Miller 1983).

Almost all investigations of song matching and repertoire use have involved playback experiments and measures of response strength to the tape recorded songs. Ideally, field studies to determine the occurrence and significance of song sharing (without using controlled playback experiments) would be on birds with only one or two songs in their repertoires. Usually, though, this is not the case. Therefore a major design consideration in natural observational investigations is first to make comprehensive studies of normal singing behavior of undisturbed birds. That is, the song repertoires (and the possible differential use of songs from within the repertoires) of all subjects must be thoroughly analyzed, and the probabilities that each bird will sing a given song in different circumstances determined. Simply describing the composition of the bird's repertoire is not adequate.

Studies of the birds' natural use of song types are complicated by additional considerations. The observer's method of determining degree of song similarity may greatly influence the results. Also, some birds are known to use different song types according to: location within their territory (Lemon 1968b; Lein 1978; Schroeder & Wiley 1983a), whether a male or female is present (Smith et al. 1978; Schroeder & Wiley 1983b), distance from rival conspecifics (Simpson 1985); familiarity with the neighboring male (Wunderle 1978; Falls et al. 1982); similarity of rival male's song to self song (McArthur 1986), rate of song type switching (Simpson 1985), acoustic degradation over

distance (Morton 1982; McGregor et al. 1983); overall aggressive
motivation (Lein 1978; Schroeder & Wiley 1983a); and stage in breeding
(Falls & Brooks 1975; Petronovitch et al. 1976). Furthermore, three
recent studies have shown that the intensities of agonistic interactions
were not correlated with the choice of song types per se, but rather
with the rate of song type switching alone (Kramer et al. 1985; Simpson
1985) or together with the degree of matching (Horn & Falls 1986).

Thus, what may appear to be unambiguous results from studies of how
birds use their repertoires, including song matching during
countersinging, should be carefully evaluated. Some recent studies
have, however, more scrupulously investigated countersinging and song
type use in general based on detailed analyses of repertoire composition
and contextual use (McGregor & Krebs 1982; Schroeder & Wiley 1983a,
1983b; Simpson 1984, 1985; Lemon et al. 1985).

The purpose of these introductory remarks is several-fold. First, a
field study seeking to describe and interpret the function of repertoire
sharing and countersinging is likely to be more complicated than is
intuitively obvious. The design must consider many variables that may
be difficult, if not impossible to control. Secondly, I introduce this
section on the countersinging of Scott's seaside sparrows with these
remarks in order that the reader may realize why I present only
descriptive summaries rather than the testing of the significance of
repertoire sharing and matched countersinging.

Methods of investigating repertoires

When birds countersang during time budget observations, I noted
whether they matched or not, in addition to taking my standard singing
behavior measurements (bird's identity, presence or absence of

intruders, time singing, perch changes while singing, and incidence of song type switching). As described in the "General Methods," I tabulated in detail 103 time budgets (selected for comparability of date, weather, absence of intruder, etc.) for 30 mated males observed Apr-May 1981-1984.

Results and discussion of repertoire use

I measured parameters of solo primary and countersinging activity of Scott's seaside sparrows (Table III-3). The mean total singing activity (solo singing and countersinging) for males was 12.29 min song/h.

Two to four males often participated in bouts of countersinging, the alternation of songs separated by 3-8 sec (Fig. III-9). The pattern of song alternation was usually regular, but in 3% of the countersingng bouts the alternating songs drifted out of phase and began to overlap. Countersinging comprised about half of the total singing time. Approximately two-thirds of the total countersinging time was matched countersong (Table III-3).

The mean song repertoire size of the 30 males was 2.41 songs/bird/season. I did not measure the proportional use of song types within repertoires, nor did I measure the degree of repertoire sharing within the population.

Some conclusions are apparent from the data presented in Table III-3, even without statistical testing. First, apparently neither solo singing nor countersinging was preferred in the several contexts analyzed. That is, countersinging did not seem to be used proportionately more often than solo singing at territory edge, nor did perch and song type switches seem to be correlated more or less strongly with countersinging. The same lack of differential patterns according

to context seemed to exist when comparing matched to non-matched countersinging. A possible exception is that birds may have sung more minutes of matched song than non-matched song at territory edges.

Of course more comprehensively analyzed data are needed before statistically valid statements regarding repertoires and countersinging in seaside sparrows can be made. I do, however, conclude the following at this time. First, countersinging is a form of vocal "duelling" that indicates a slightly elevated aggressive or aroused state. That is, countersinging is a graded signal in seaside sparrows, but probably a less strongly graded signal than in most birds. Second, song matching while countersinging and repertoire sharing in general in these birds are probably chance events, analogous to the "epiphenomena" of song pattern variety suggested by Wiens (1982) for sage sparrows (Amphispiza belli). Songs of seaside sparrows may be observed to match simply as a consequence of their small repertoires of simple and similar songs, their low population turnover rates, and their sedentary habits.

Flight Songs: Description and Comparison to Perch Songs

Description

An early Florida naturalist, Donald J. Nicholson aptly characterized seaside sparrow singing: "Towards the end of March the marshes are fairly buzzing with the purring, wheezing songs...He tries one perch and seeks another fifty or seventy-five yards away flying low over the rank growth. Every so often he fairly 'explodes' with passion leaving his concealment to rise on fluttering wings sixty or seventy feet above the marsh uttering his erratic little song as he goes up and down dropping out of sight in the salicornia" (Nicholson 1946, p. 41).

The flight song (Fig. III-10), accompanying the flight song display, is a combination of preliminary calls followed by the primary song. This vocalization and display of about 3-4 sec is sporadically given by males throughout the breeding season. It begins with introductory high-pitched "si" calls, followed by lower-pitched "tuck" calls, and ends with one or two condensed versions of the primary song. The buzzy trill of the primary song portion is about 0.4 sec shorter than the trill of the normal primary song. The introductory calls vary in duration and type, but are always given on the ground and during the bird's ascent to about 10-15 m. The primary song is uttered as the bird descends. Woolfenden (1956), Trost (1968), Post & Greenlaw (1975), and Werner & Woolfenden (1983) also describe singing and flight songs of seaside sparrows.

Methods of investigating flight song activity

My observations of Scott's seaside sparrows during the breeding seasons of 1981-1982 suggested that overall song activity seemed to be affected by whether the birds were mated, and by time of day, time of year, and weather. In most Passerines these factors do influence the intensity of primary song singing from a perch (hereafter designated in this section as "perch singing"). I measured and compared perch song and flight song activities of my study population during the early breeding season of 1982. Then I tested whether the above factors differentially affected flight song activity (as compared to perch singing) by comparing the relative frequencies of flight songs to perch singing under specified conditions described below.

I sampled the overall singing activity of 28 males during 31 field days from 12 Feb-26 Apr 1983. Throughout the day I monitored flight

song and perch song activity within one hour time blocks from pre-dawn through mid-afternoon. The time blocks were designated in hours relative to sunrise: the first hour block of a day began 15 min before sunrise, the second hour block began 45 min after sunrise, and so on. I randomly chose and timed the perch singing of a different male during each hour block. Simultaneously, I counted all flight songs heard within 100 m during the hour. As I counted and timed songs during each hour block, I also noted wind velocity, temperature, the singing bird's location, and identity and mated status (if known).

In summarizing my data, I defined an hour's "flight song activity" as the average number of flight songs heard within the 100 m radius during the hour. I defined "perch song activity" as the average number of minutes the randomly chosen birds sang during the hour within the same 100 m. Then, for every level of increment of the variables being investigated (e.g. for temperature category $5-9^{\circ}$ C), I tabulated flight song activity (FS), perch song activity (PS), and a calculated FS/PS ratio. A statistical analysis using multiple regression would have been the ideal method of exploring these data. Yet because some data were ordinal rather than interval and normality was not assumed, non-parametric statistical analyses were required. In order to validly consider the effect of only one variable at a time, I chose subsets of data, as described below for each analysis. I used Spearman rank correlation (Siegel 1956) to determine if PS, FS, and FS/PS ratios were correlated with day of year, time of day, temperature, and wind velocity. I tested significance of the correlation coefficient at the two-tailed $\underline{P} < 0.05$ level. I also compared FS and PS activities of mated and unmated birds with a two-tailed $\underline{X}^2$ one-sample test (Siegel 1956).

Results of singing activity analysis

Males sang perch songs at an overall rate of 17.1 (SE=5.9) min song/h. Flight song rate varied considerably among males. The mean rate was 0.15 flight songs/male/h. The rates of perch songs, flight songs, and FS/PS ratios did, however, vary significantly as detailed below.

Four variables correlated significantly with both perch singing and FS/PS ratios: day of year, time of day, temperature, and wind velocity. Mated and unmated birds differed significantly in the number of flight songs given.

Day of year. I analyzed the following subset of data to determine the correlation of singing activity with day of year: 88 h of measurements for unmated birds taken on 19 days when the temperature was 15-24° C and the wind was <24km/h. I found that perch song activity increased significantly (r=0.72), and FS/PS ratios (r=-0.81) decreased significantly as the breeding season progressed, up until the last week of April. Flight song activity considered alone, however, did not correlate significantly with day of year (r=-0.01).

Time of day. I determined the effect of time of day by considering the same subset of observations: 88 hours of measurements for unmated birds noted when the temperature was 15-24° C and the wind was <24km/h. I found perch song rate was greatest just after sunrise and declined significantly (r=-0.95) as the day progressed (excluding evening singing). Flight song activity remained about the same all day, although the FS/PS ratio increased significantly (r=0.83) through the day (Fig. III-11).

Wind. I analyzed the following subset of data to determine the effect of wind: 79 morning hours (hour blocks 1-5) of measuremets for

unmated birds noted when temperatures were $15-24^{\circ}$ C. I found that brisk winds had a definite dampening effect on perch song activity ($r=-0.97$) but no significant effect on flight song activity. The FS/PS ratio increased significantly ($r=0.88$) as wind velocity increased (Fig. III-12).

Temperature. To determine the influence of temperature, I considered 77 hours of observations made on unmated birds, during hour blocks 1-4, and when the wind was <24km/h. I found that cooler temperatures significantly ($r=0.88$) decreased perch song activity but had no significant effect on flight song activity. The FS/PS ratio did significantly decrease ($r=-0.83$) as temperature rose (Fig. III-13). In other words, as with high winds, birds gave proportionally more flight songs in cooler weather.

Mated status. I considered the singing activity of 23 males before and after they were mated. The time elapsed between measurements was 8-19 days. I observed birds for 73 h during hour blocks 1-4, when temperatures were $15-24^{\circ}$ C and the wind was <24km/h. Males sang less (14.9 min/h) after they were mated than before mated (19.7 min/h), but this decrease in singing may have been at least partially due to the seasonal decline in singing activity described above, or vice versa.

From a sample of 122 flight songs, 74 were given by birds of known mated status. Unmated birds sang 84% of these 74 flight songs (Fig. III-14). This difference was highly significant (two-tailed $\underline{x}^2$ one-sample test, $\underline{x}^2=33.8$, $\underline{df}=1$, $\underline{P}<0.001$).

Discussion of flight songs

Flight songs are characteristic of birds that live in open grasslands or tundra. Many emberizine sparrows, including the

congeneric seaside, sharptail, Baird's (A̲. bairdii), and Le Conte's sparrows (A̲. leconteii), have well-developed flight songs.

Why do seaside sparrows give flight songs? Although the flight song is a highly conspicuous vocalization, obviously its energetic cost is greater than that of perch singing. Post & Greenlaw (1975) report that in their migratory northern seaside sparrows, flight songs are much more common soon after females arrive on their male's territories. This, as well as my findings that unmated Scott's seaside sparrows gave more flight songs than mated birds, suggests that flight songs may be used in mate attraction. All seaside sparrows, however, continue to give these vocalizations throughout the breeding season.

A major portion of the flight song vocalization is the uttering of one or two modified primary songs. Elsewhere (Chapter IV) I have shown experimentally that the primary song is essential for both mate attraction/retention and territory establishment/retention. Thus, it is reasonable to assume that flight songs can effect the same critical functions. I have presented evidence that birds give relatively more flight songs (and sometimes they give only flight songs) during inclement weather and when unmated. I therefore suggest that even though they may be energetically costly, flight songs so effectively magnify the message of the primary song that they are worth more to the male, especially under otherwise adverse singing conditions.

Figure III-11. Relationship between time of day and the ratio of Flight songs/Perch singing.
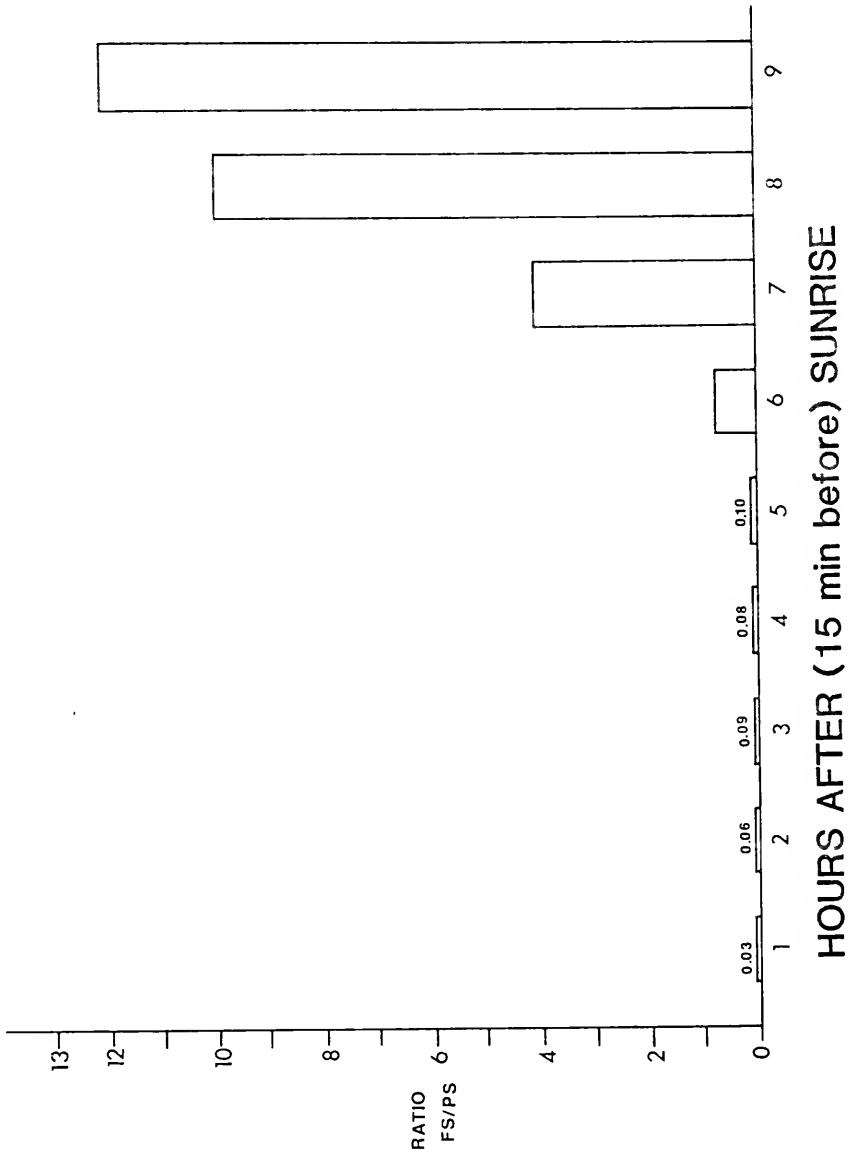
Figure III-12. Relationship between wind velocity and the ratio of Flight songs/Perch singing, as defined in text. The first bar indicates the FS/PS ratio when there was no wind; the second bar indicates the ratio when the wind was 1-8 km/h; the third, 9-16 km/h, and so on.
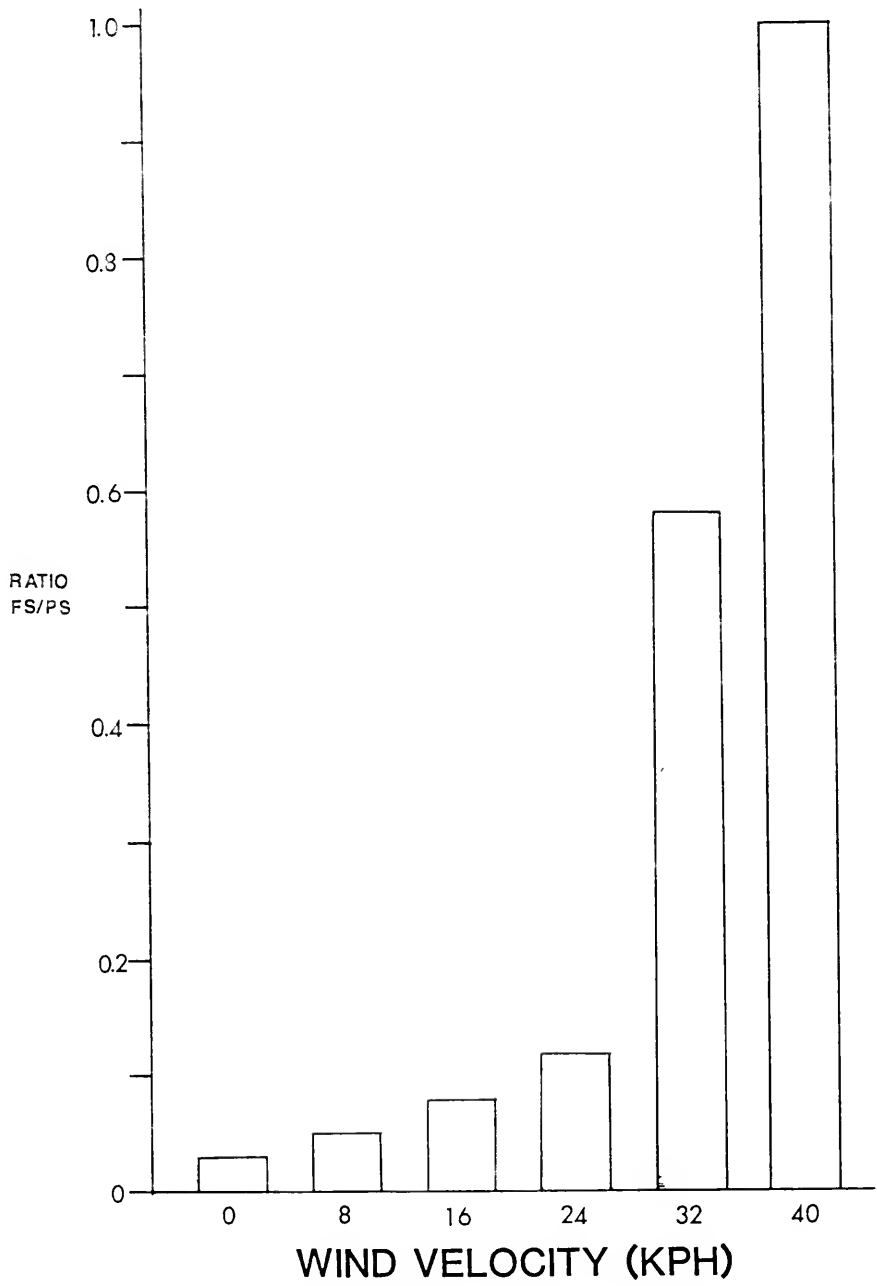
Figure III-13. Relationship between temperature and the ratio of Flight songs/Perch singing, as defined in text. The first bar indicates the FS/PS ratio when the temperature was 5-9° C; the second bar indicates the ratio when the temperature was 10-14° C, and so on.
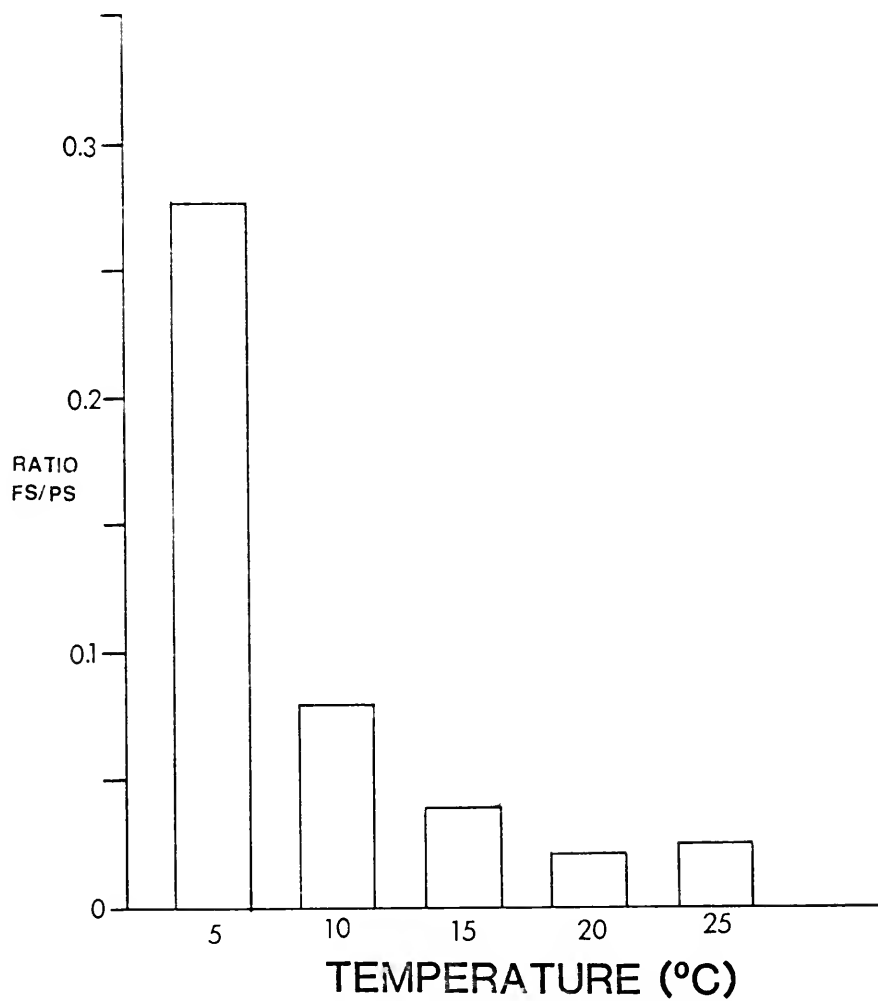
Figure III-14. Number of Flight songs recorded in early 1983, given by birds of designated mated categories.
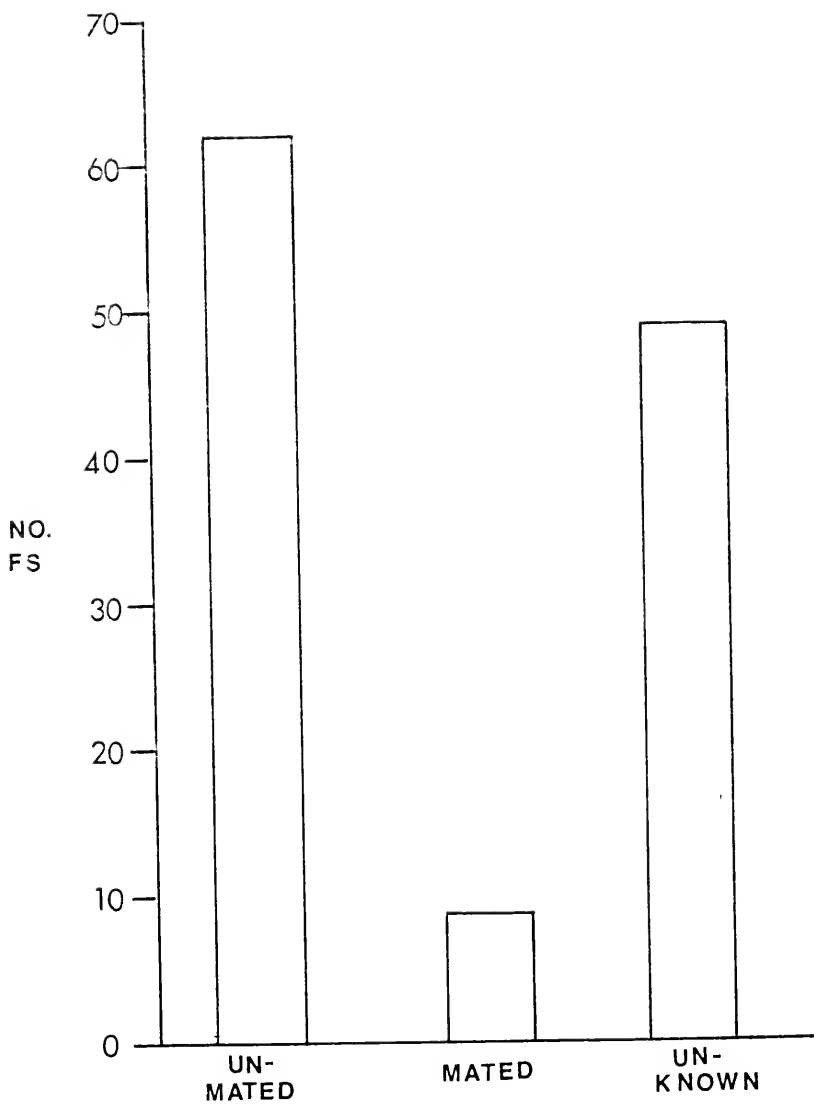
Introduction

"Why do birds sing" is one of the oldest questions in ornithology. Song meaning and function (Smith 1977) vary among bird species and sometimes within species. Meaning is the combined product of signal and context manifested as a change in behavior; function is the way in which the behavioral change benefits the signaler by ultimately contributing survival value and promoting reproductive success.

Functions of avian vocalizations, including calls, are reviewed by Thielcke (1970). Song is used primarily for territorial establishment and defense, mate attraction and maintenance of pair bond, coordination of reproductive behavior between mates and within the population, signaling motivation, and species and individual recognition (Beer 1982). The role of song in individual recognition is discussed by Falls (1982), and the function of song in species recognition is reviewed in Becker (1982).

The "dual function of song" hypothesis prevails in most explanations of why birds sing: a male bird sings to establish and maintain a territory and to attract and retain a mate. Early writers emphasized the apparent dichotomy between mate attraction and territorial function (reviewed in Armstrong 1973). These two proximate functions, however, are not necessarily mutually exclusive; both can be accomplished simultaneously. Tinbergen (1939) made this clear and proposed the term

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"advertising song." The duality of song function and its ultimate role
in promoting reproductive success are reviewed in Catchpole (1982).

I directly tested the dual function of song hypothesis with field
experiments in which I temporarily muted male seaside sparrows. I chose
this approach for the following reasons. A significant design problem in
the study of bird song has always been how to separate the auditory
component of song from the visual stimulus of the vocalizing and
displaying bird. One can remove the bird and replace it with recorded
song, or remove the song from the bird. Using the first approach, many
excellent studies have indirectly tested the role of song with
combinations of male removals, models, and playback experiments
(Catchpole 1977; Krebs 1977b; Krebs et al. 1978, 1981; Yasukawa 1981;
Kramer et al. 1985). The second approach--experimentally muting birds
in the field--has been reported for only one species, red-winged
blackbirds.

Peek (1972) and Smith (1976) permanently muted male red-winged
blackbirds by sectioning the hypoglossal nerve. They found that muted
birds suffered heightened territorial losses and trespass rates,
compared to sham-operated control birds. For several reasons it was
difficult to determine to what extent the muted males were less
successful in attracting and retaining mates. Red-winged blackbirds are
polygynous, and females may discriminate among males on the basis of
territory quality (Smith 1972; Holm 1973; Lenington 1980). Only limited
anecdotal information on mate retention was reported for these muting
experiments. The authors also pointed out that the muted birds'
behaviors were influenced by the administration of anesthesia and by
respiratory impairment.

In 1976 and 1979 Smith described a different field muting technique that overcame the complications of anesthesia and respiratory distress. Without using anesthesia, he temporarily muted red-winged blackbirds by cutting the membrane of the interclavicular air sac, one of the air sacs that propels air into the syrinx. Although Smith used only one sham and three experimental birds, his results suggested that there were more intrusions on the territories of muted males, and that muted birds used the "sidling" visual display more frequently than before they were muted. As in the previous experiments, it was unclear whether females reacted differently to muted versus non-muted males.

In designing a test of song function, I sought to avoid the complications of previous field muting experiments. I used a modification of Smith's temporary muting technique, with larger sample sizes controlled for time of breeding season, and collected more quantitative data. Furthermore, I used a species more representative of songbirds in general. Extrapolating from the experiments on red-winged backbirds is problematic because, as already mentioned, they are polygynous, and also sexually dimorphic, actively displaying birds whose visual behaviors are used in conjunction with their vocalizations. In contrast to red-winged blackbirds, monogamous and cryptically-colored seaside sparrows have few visual displays. They nest in dense vegetation where visibility is reduced. Being songless should have an especially marked effect on seaside sparrows, whose "displays" are virtually all acoustic.

My muting experiments specifically tested the two predictions of the dual function of song hypothesis: 1) Male seaside sparrows sing to

attract and retain mates; and 2) Male seaside sparrows sing to establish
and maintain territories.

Methods

Project history, subjects, and study site were discussed in Chapter
II.

Experimental Design

Muting experiments simultaneously tested the predictions of the dual
function of song hypothesis: female attraction/retention and territory
acquisition/maintenance. The experimental design is summarized in Table
IV-1.

I administered two rounds of temporary mutings (and sham-operations)
in 1983 and 1984. Each round was preceded and followed by time budget,
mated status, and other observations of the experimental (Muted),
control (Sham-Operated), and Undisturbed birds. The first round of
mutings (Early Season: 1-3 Apr 1983; 17-23 Mar 1984) allowed comparison
of the proportions of Muted birds acquiring mates and territories to the
proportions of Sham-Operated and Undisturbed birds acquiring mates and
territories. The second round of mutings (Mid-Season: 27 Apr-5 Jun
1983; 1-25 May 1984) permitted investigation of the role of song in mate
retention and in territorial integrity. These second round experiments
allowed measurement and comparison of: incidence of intrusion and
reaction to intruders; repulsion success; reaction to playback
(simulated intrusion); loss or retention of territory; territory
boundary change; mated status change; and time spent in singing and
other vocalizations and behaviors (Table IV-1). Some of these measured

Table IV-1. Experimental design of muting experiments

Muting   Event/Behavior Measured[a,b]
Round

Early-   Female attraction
Season   Territory acquisition

Mid-   Female retention
Season   Territory retention
        Territory size change (m^2)

     <u>Behaviors Measured When No Intruder Present</u>[c]
        Primary song (or attempt) time
        Whisper song time
        Countersong time (matched)
        Countersong time (not matched)
        Tuck call time
        Tuck/Tsip call time
        Si Twitter call time
        Tchi/Tyu call time
        Zuck call time
        Tchi flight frequency
        Flight song frequency

        Female (mate) on territory time
        Female (mate) aggressive call time
        Female (mate) chase intruder time
        Female (mate) solicitation call time

        Associate/copulate with female time
        Feeding, resting, and off territory time

     <u>Behaviors Measured While Intruder Present</u>[c]
        Intrusion occurrence frequency
        Repel intruder frequency
        Not repel intruder frequency
        Total intrusion time
        Intrusion time >5 m between birds
        Intrusion time 0.5-5 m between birds
        Intrusion time <0.5 m and contact

        Primary song (or attempt) time
        Whisper song time
        Countersong time (matched)
        Countersong time (not matched)
        Tuck call time
        Tuck/tsip call time
        Si twitter call time

Table IV-1--continued

Mid-
Season-   Event/Behavior--continued
cont.

Behaviors Measured While Intruder Present[c]--continued

    Tchi/Tyu call time
    Zuck call time
    Tchi flight frequency
    Wing raise time
    Chase time
    Grass pick time
    Sham-preen time
    Bob and bill jab time

Behaviors Measured During Playback Experiment
    Primary song (or attempt) time
    Whisper song time
    Countersong time (matched)
    Countersong time (not matched)
    Tuck call time
    Tuck/tsip call time
    Si twitter call time
    Tchi/Tyu call time
    Zuck call time
    Tchi flight frequency
    Wing raise time
    Chase time
    Grass pick time
    Sham-preen time
    Bob and bill jab time

    Latency of reaction time
    Within 25 m model time
    Within 5 m model time
    Within 0.5 m model time
    Contact model frequency

[a]Changes in Muted birds' territory sizes were compared Before-During,
and During-After their songless states and tested with one-tailed
Wilcoxon matched-pairs signed-ranks tests (WSR). Behavioral changes were
compared Before-During (but not During-After) with two-tailed Wilcoxon
matched-pairs signed-ranks tests.

Table IV--continued

[b]Differences between the groups' (Muted, Sham-Operated, and Undisturbed) abilities to acquire and retain mates, and acquire and retain territories compared with X^2 or Fisher exact probability tests. Because size change in one treatment group may cause concurrent size change in another group, territory size comparisons among the 3 groups should not be made with X^2 or Mann-Whitney U-tests, which assume independence of groups. Thus one-tailed Wilcoxon matched-pairs signed-ranks tests are used to compare indirectly size changes for treatment groups (see text). Behavioral differences between the groups (Muted to Sham-Operated, and Sham-Operated to Undisturbed) compared with two-tailed Mann-Whitney U tests (MWU).

[c]Frequency measured as occurrences/hour. Time measured as minutes/hour.

behaviors were only rarely seen; thus similar behaviors were grouped for statistical analyses of results.

I made two types of comparisons for each round of mutings. First I compared treatment groups: Muted to Sham-Operated and also Sham-Operated to Undisturbed. Additionally, I was interested in how being muted affected a bird; therefore I made Before, During, and some After comparisons for the individuals.

My experimental protocol was as follows. After preliminary observations on birds as they began to sing in early February, I designated approximately 30 males each year to be Muted, Sham-Operated, or Undisturbed birds for the Early Season round, and then re-designated a treatment for the Mid-Season round. The treatment assignment was random, except: no bird underwent the same treatment twice; territories of muted birds were not contiguous; and only mated males were assigned a treatment and studied in the Mid-Season round.

I chose the dates of the Early Season manipulation each year according to when heightened male-female pairing behavior began. Birds were also in the process of establishing territories at this time. They had preliminary territories, but boundaries were not fixed and changes in ownership sometimes occurred during those early spring weeks. I considered "territory acquisition" to be successful defense of any area on the study site (or the censused adjacent marsh) within 0-10 days after manipulation.

For both rounds of manipulation, I observed each of the subjects at least every third day for a total of ≥ 20 h (or more) per season. Behavioral data used for analyses were those collected 0530-0930 and under moderate weather conditions. Muted and Sham-Operated birds were

studied more intensively just before and after their surgery. I drew
territorial maps during every observation period and described
behavioral events in detail on cassette tapes and field data forms. I
later transcribed notes and tabulated and analyzed the data.

To investigate further behavior under more controlled conditions, I
simulated territory intrusion with playback experiments. I hid a
playback tape recorder at the approximate center of the bird's territory
and placed a stuffed model seaside sparrow in Juncus 1 m above the
ground. The seaside sparrow playback song had been recorded in 1981, 2
km from the study site. It was recorded on a Sony TC 150 cassette
recorder (Mineroff-modified) with a Bell and Howell "Shotgun"
unidirectional electret condenser microphone with wind screen. The song
was played back with the same recorder at what I estimated to be a
normal song volume. The playback period consisted of 7 min blank tape,
8 min song, and 15 min blank tape. I tested all Muted, Sham-Operated,
and Undisturbed birds on three occasions: Before (1 day prior), During
(3 days following), and After (20 days after) their manipulations.
Reactions listed in Table IV-1 (Playback Experiments) were noted during
the 30 min experiment while the tape ran. For comparative purposes,
playback experiment results were standarized, from min/0.5 h playback to
min/hour by multiplying by two.

Additional recordings of vocalizations were made with the equipment
described above. Audiospectrograms were prepared on a Kay Elemetrics
7029A Sona-graph (wide-band [300 Hz] filter and 80-8000 Hz scale).

Muting Procedure

Birds muted or sham-operated were first caught in mist nets on their
territories. After surgery I carried the bird back to his territory and

released him. I used a modification of Smith's technique of temporarily muting the bird by rupturing the interclavicular air sac membrane (Smith 1976 and 1979). In pilot work, my first attempts to mute birds in the laboratory and field were unsuccessful for several reasons. I had difficulty adjusting the anesthesia dosage to a level that would relax the bird yet not persist for hours, thus exposing the bird to predation, inclement weather, and food deprivation. I decided that the most humane and experimentally straightforward alternative was to perform the surgery quickly and without anesthesia, which enabled me to release the bird back on his territory within 15 min after capture. Another source of early failure was my closing the skin incision with too many sutures, thus offsetting the desired effect of rupturing the air sac to direct air away from the syrinx.

I present a stepwise instructional outline of my temporary muting procedure:

1. Hold the bird in one hand and work with the other. Keep the head and wings from getting in the way with fingers of your holding hand.

2. Part the feathers in the area of the furculum and neck, then swab with antiseptic. I used Betadine solution (Purdue Frederick Company).

3. Mat down the parted feathers with water-soluable lubricating jelly. This step is unnecessary if one works quickly enough so that the wet antiseptic holds the feathers away from the incision.

4. Make a skin incision from the base of the furculum extending rostrally about 1.2 cm. I used a new #12 scalpel blade.

5. Push aside connective tissue with blunt forceps and expose the interclavicular air sac.

6a. To mute birds: Grasp the air sac and puncture it. I found this somewhat difficult--the air sac is thin, slippery, and rapidly rising and falling in a breathing bird. To make the initial 1 mm puncture, I used the slightly bent tip point of a #12 scalpel blade, then widened the hole to about 1 cm by inserting and spreading small forceps. One must be careful at this step--the small carotid arteries and other vessels lie just beneath the air sac. Keep a styptic pencil handy for bleeding emergencies.

6b. To sham-operate birds: Touch the air sac with forceps.

7. Close the skin incision with one suture. I used a sterile 0.5 inch circular cutting-edge needle attached to 5-0 silk suture.

8. Swab again with antiseptic and comb the feathers back into place.

After practice I was able to perform this procedure in the field in less than five minutes. Of my total 57 field Muted and Sham-Operated birds, only four were known or presumed to have died as a direct consequence of the surgery--two died during surgery and two permanently disappeared after release.

Statistical Analyses

Non-parametric statistics were used for all analyses (Siegel 1956; Conover 1980). I compared mate attraction and retention, and territory acquisiton and retention with X^2 contingency (or Fisher exact probability) tests. The individual's Before and During behaviors were compared with two-tailed Wilcoxon matched-pairs signed-ranks tests. Wilcoxon tests were also used to compare Before, During, and After territorial size changes. Because territorial size change in one treatment group (Muted, Sham-Operated, or Undisturbed) probably caused a concurrent size change in another group, comparisons of size changes

among the 3 groups could not be made with $\underline{X}^2$ or Mann-Whitney $\underline{U}$-tests, because both assume independence of groups. Therefore I indirectly tested the significance of territory and size changes between groups using Wilcoxon tests. That is, I noted whether there was a significant size change from Before to During in the Muted group and whether there was a significant size change in the Sham-Operated group from Before to During. Territorial loss was included in this analysis by considering it to be a size change from the original area to 0 m^2 area. Likewise, in the analysis of size change from During to After, permanent territorial loss was considered to be an expansion of 0 m^2 in area. All other group comparisons (Muted, Sham-Operated, and Undisturbed) were made with Mann-Whitney $\underline{U}$ tests.

Results

Voice and Post-Operative Recovery

I found Muted and Sham-Operated birds back on their territories a few hours to two days after their surgery. Sham-Operated birds sang and apparently behaved normally in every respect. Comparisons between Sham-Operated and Undisturbed groups revealed only one significant difference among all of the attributes listed in Table IV-1. Thus, Undisturbed birds were pooled with Sham-Operated birds for some statistical tests, as noted.

Two unexpected yet fortuitous outcomes of the muting manipulation were: 1) Muted birds attempted to sing by going through the motions of singing; and 2) Muted birds gave all of their normal calls. Thus these birds were actually "de-songed" rather than completely "muted," although for convenience I use the latter term throughout this paper.

By Day 5 following surgery most of the muted birds began to utter croaks and squeaks as they attempted to sing. Nearly all Muted birds fully recovered their reportoire of 2-3 distinct song types by Day 12. Fig. IV-1 shows the audiospectrogram of Before song, and Fig. IV-2 shows the During "song" of a muted bird. Within 10 days after surgery skin incisions healed completely and the suture dropped out. I never detected any infection or other detrimental consequence of the surgery other than the mortality mentioned above.

Mate Attraction and Retention

Results of the Female Attraction and Female Retention tests clearly indicate the importance of song in obtaining and retaining a mate (Fig. IV-3). None of the 10 Early Season Muted birds had obtained a mate by Day 7 after surgery, as contrasted to 11 of the 13 Sham-operated and 32 of the 37 Undisturbed birds having mates by then. The difference between Muted and Sham-Operated birds is highly significant (one-tailed Fisher exact probability test, $\underline{P}$<0.0001).

All female mates of the 21 Mid-Season muted birds began ignoring their mates immediately following manipulation. These females did, however, continue giving solicitation calls at about the same frequency and remained on the territory for 1-2 days. By three days post-muting, most females deserted their mates and paired with intruders or neighboring males. Only one muted bird retained his female beyond three days after manipulation. I never saw her associating with her mate; she probably stayed on his territory because she had a nest with hatchlings. This mate retention difference between treatment groups is also highly significant (one-tailed $\underline{X}^2$ 2X2 test, $\underline{X}^2$=59.6, $\underline{N}$=21 Muted and 13 + 30 pooled Sham-Operated + Undisturbed birds, $\underline{df}$=2, $\underline{P}$<0.001).

Figure IV-1. Audiospectrogram of bird ABOR recorded 3 days prior to muting.

kHz

TIME IN SECONDS
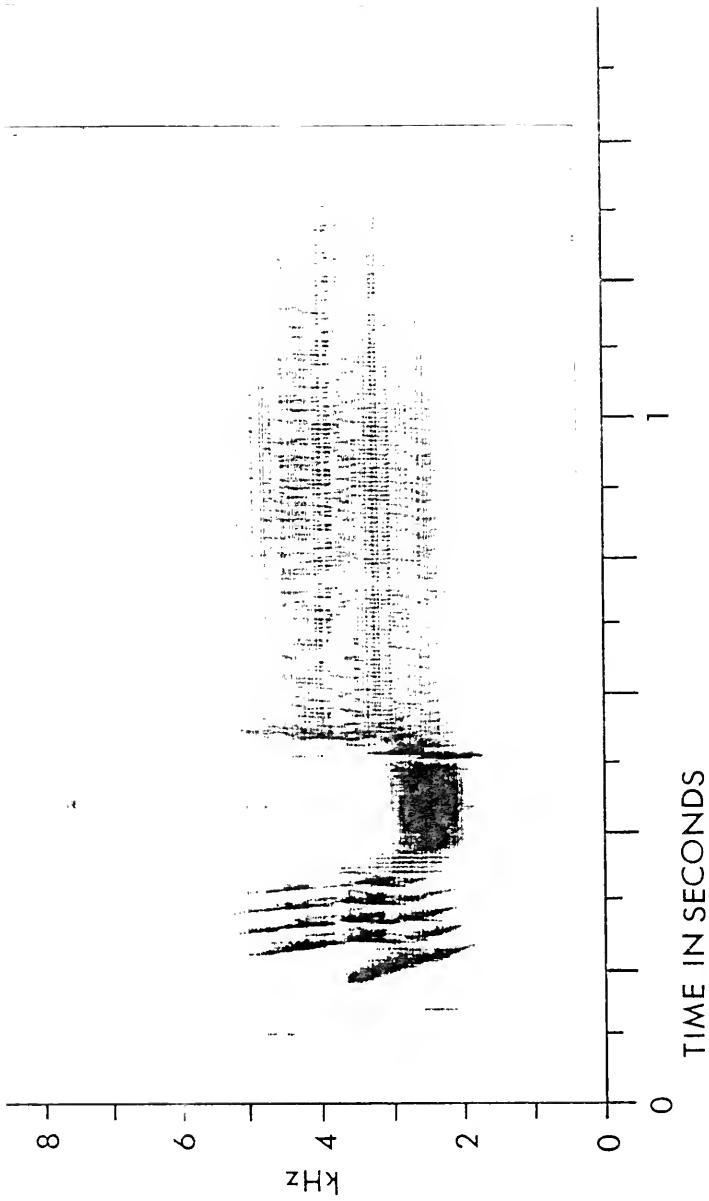
Figure IV-2. Audiospectrogram of "songs" of muted bird ABOR recorded 5 days after muting.

TIME IN SECONDS
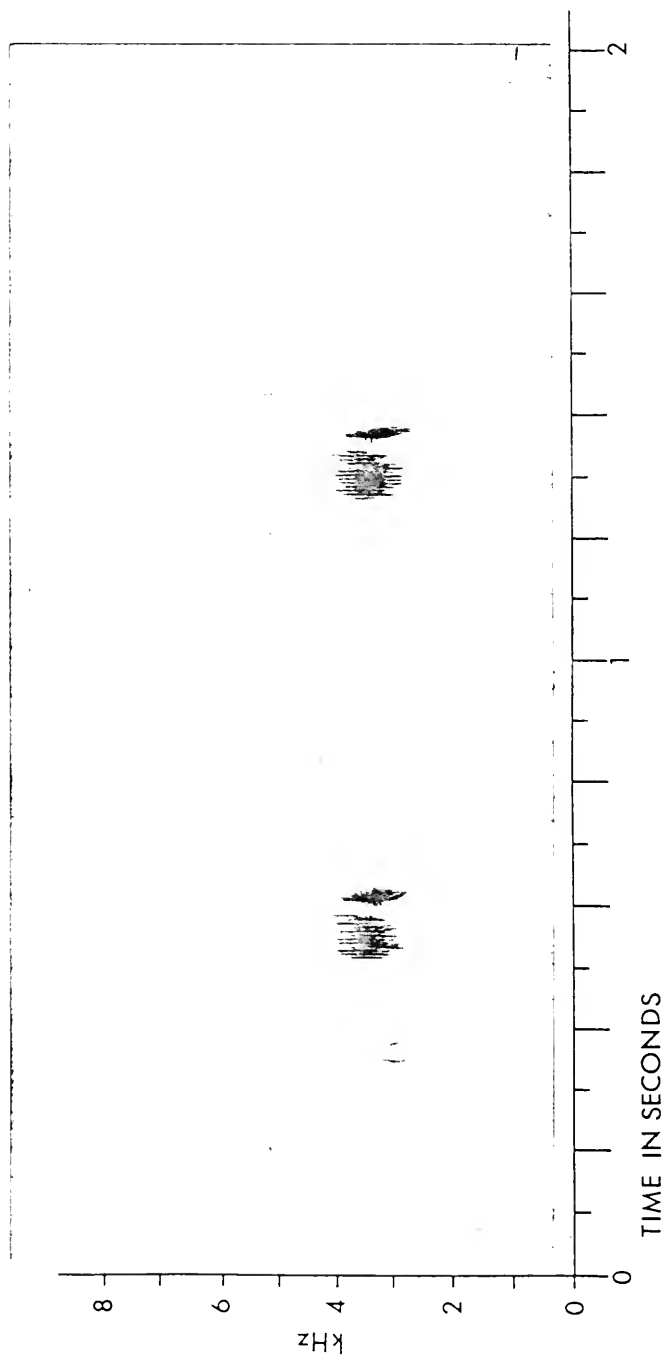
Figure IV-3. Relative abilities of Muted versus Sham-Operated and Undisturbed males to attract (A) and retain (B) females, 1983 and 1984 combined. Sample sizes as given.
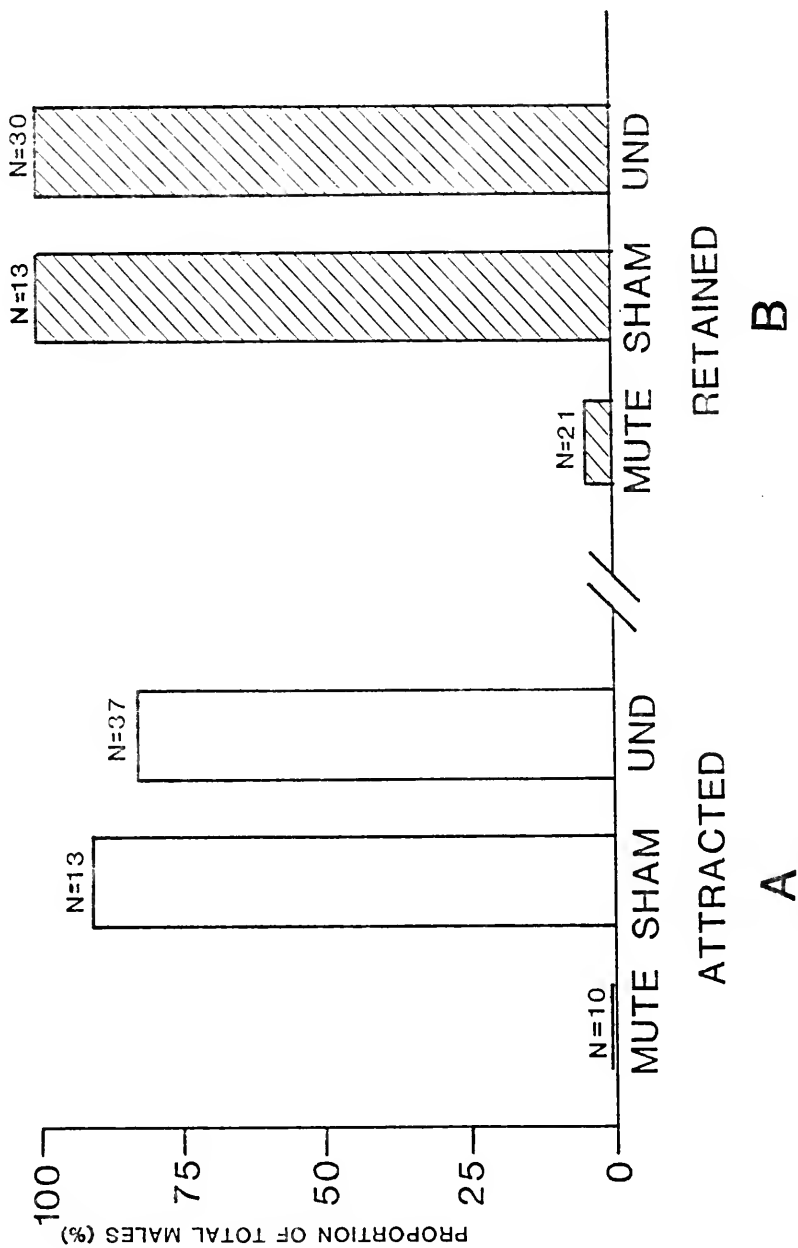
Table IV-2. During songless comparison of territory ownership and size changes for the Mid-Season mutings

	Change					
Treatment	Sample Size	Lost Terr.	Smaller Terr.	Expanded Terr.	No Change	Mean Size Change
Muted	21	6	15	0	0	−79%**
Sham-Operated	13	0	1	10	2	+44%**
Undisturbed	30	0	0	17	13	+31%**

**Significant size change from Before to During, one-tailed Wilcoxon matched-pairs signed-ranks test, $\underline{P}$<0.005. Also see text.

Table IV-3. "After song regained" comparison of territory ownership and size changes for the Mid-Season mutings

			Change				
Treatment	Sample Size	New Terr.	Smaller Terr.	Expanded Terr.	"Shared" Terr.	No Change	Mean Change
Muted	21	3	0	14	3	1	+76%*
Sham-Operated	13	0	8	0	0	5	-13%*
Undisturbed	30	0	12	0	0	18	-15%*

*Significant size change from During to After, one-tailed Wilcoxon matched-pairs signed-ranks test, $\underline{P}$<0.005. Also see text.

Territory Establishment, Retention, and Size Change

Territory acquisition was delayed for the songless males. None of the 10 Early Season muted birds had obtained a territory by 10 days after manipulation, in contrast to 10 of the 13 Sham—Operated and 23 of the 37 Undisturbed birds. This difference was highly significant (one-tailed $\underline{X}^2$ 2X2 test, pooled Sham—Operated + Undisturbed, $\underline{X}^2$=25.4, 1 $\underline{df}$, $\underline{P}$<0.001). Eight of the muted birds eventually obtained territories by 12-29 days (mean = 18.2) after surgery.

The Mid-Season post-muting changes in territorial ownership and sizes are summarized in Tables IV-2 and IV-3. Six muted birds incurred territory losses during the time they remained songless compared to no Sham—Operated or Undisturbed birds losing their territories. This is a highly significant difference (one-tailed Fisher exact probability test, N=21 Muted and 13 + 30 pooled Sham—Operated + Undisturbed birds, $\underline{P}$<0.001). Expansion of adjacent Sham—operated and Undisturbed birds' territories caused significant territory size decrease for the remaining 15 muted birds. This territory size decrease for Muted birds from Before to During was highly significant (one-tailed Wilcoxon matched-pairs signed-ranks test, $\underline{T}$=0, $\underline{N}$=21 paired observations, $\underline{P}$<0.005). There was a Before to During significant size increase for both the Sham—Operated ($\underline{T}$=2, $\underline{N}$=13 paired observations, $\underline{P}$<0.005) and Undisturbed groups ($\underline{T}$=0, $\underline{N}$=30 paired observations, $\underline{P}$<0.005).

Territorial changes at 10 days after the Muted birds regained their singing ability were also evident (Table IV-3). Many ex-muted birds expanded nearly to their original territorial boundaries. Three established new territories, and three remained on ("shared") their original territories, seemingly behaving subdominant to the males that

had taken over these territories. One-tailed Wilcoxon tests indicated a significant size increase for ex-muted birds ($\underline{T}=0$, $\underline{N}=17$ paired observations, $\underline{P}<0.005$) and significant size decreases for Sham-Operated ($\underline{T}=0$, $\underline{N}=8$ paired observations, $\underline{P}<0.005$) and Undisturbed birds ($\underline{T}=0$, $\underline{N}=18$ paired observations, $\underline{P}<0.005$).

Behavioral Changes of Muted Birds

I compared Muted birds' behaviors Before and During their songless states, and also compared the behavior of Muted to Sham-Operated and Sham-Operated to Undisturbed birds. I did not compare statistically "After" to "Before" and "During" behaviors because by the time song was fully recovered some birds of all treatment groups exhibited a marked natural seasonal decrease in territorial and other observable behavior. The results of Before and During behavior for individuals (Muted birds) and a comparison of Muted, Sham-Operated, and Undisturbed groups are given in Tables IV-4 and IV-5, respectively. Considering all comparisons, the behaviors of Sham-Operated and Undisturbed groups differed significantly in only one measurement--primary song time during intrusion. I have no explanation for this difference, other than the fact that the cummulative probablility of a Type I error becomes great when many comparisions are made.

Table IV-4. Behavior changes for individuals, from "Before" to "During" muted

Event/Behavior[a]	Individual Comparisons[b] (Muted Birds)		
	Before	During	P
(A) No Intruder Present			
Primary song (or attempt) time[c]	11.99	7.37	***
Flight song frequency	0.10	0.06	***
Tuck, Tsip, Si Twitter call time	<0.01	0.03	NS
Tchi-Tyu and Zuck call time	<0.01	0.02	NS
Female solicitation call time	0.45	0.47	NS
Associate with female time	2.03	0.00	***
(B) Intruder Present			
Intrusion occurrence frequency	0.11	3.69	***
Repel intruder frequency	0.11	0.00	***
Total intrusion time	0.42	33.20	***
Intr. time >5 m between birds	0.29	23.53	***
Intr. time 0.5-5 m between birds	0.19	8.06	***
Intr. time <0.5 m and contact	<0.01	1.61	***
Primary song (or attempt) time[d]	1.86	0.28	***
Chase time[d]	2.51	4.71	***
"Alarm/Threat" call time[d]	<0.01	1.81	***
"Attack" call time[d]	<0.01	<0.01	NS
Wing raise time[d]	2.52	4.71	**
Grass pick time[d]	0.02	0.20	***
Sham-preen time[d]	0.00	2.65	***
Bob and bill jab time[d]	0.00	0.14	***
(C) Playback Reaction			
Primary song (or attempt) time	4.59	3.84	*
Tuck, Tsip, Si Twitter time	11.10	10.77	NS
Tchi-Tyu and Zuck call time	0.10	<0.01	NS
Tchi flight frequency	0.77	0.62	NS
Wing raise time	0.59	0.79	NS
Grass pick time	0.49	0.55	NS
Sham-preen time	3.88	3.41	NS
Bob and bill jab time	0.36	0.35	NS
Latency of reaction time[e]	0.88	0.99	NS
Within 5-25 m model time	22.04	21.11	NS
Within 0.5-5 m model time	12.41	11.52	NS
Within 0.5 m model time	2.92	2.71	NS
Contact model frequency	1.01	0.91	NS

Table IV-4--continued

[a]Similar vocalizations and behaviors are grouped: Tuck, Tsip, and Si
Twitter calls ("alarm/threat calls") are given in reaction to nearby
(0-15 m) predators and avian invaders; Tchi-Tyu, Tchi, and Zuck call
("attack calls") are vocalizations often used by males and females
invading another territory; Wing raises, grass picking, sham-preening,
bobbing and bill jabbing are visual displays given in the presence of
nearby (0-5m) predators and avian invaders.

[b]Figures are mean values per bird for 21 muted birds. Minimum
observation time per bird was 10 h for (A) and (B). Time results
reported as min/h; playback results standarized to min/h. Frequency
results reported as mean occurrences/h. Individual Before-During
comparisons tested with two-tailed Wilcoxon matched-pairs signed-ranks
tests. Significance of differences between Before and After:
***P<0.01; **P<0.02; *P<0.05; NS=Not Significant.

[c]Includes countersinging with another males off territory.

[d]Standardized to min/h intrusion.

[e]Minutes from first song on tape to first observed reaction; not
standarized to min/h.

Table IV-5. Behavior differences comparing Muted, Sham, and Undisturbed groups

Event/Behavior[a]	Group Comparisons[b]				
	Mute	Sham	Und	P M/S	P S/U
(A) No Intruder Present					
Primary song (or attempt) time[c]	7.37	11.43	12.51	*	NS
Flight song frequency	0.06	0.13	0.11	*	NS
Tuck, Tsip, Si Twitter call time	0.03	<0.01	<0.01	NS	NS
Tchi-Tyu and Zuck call time	0.02	<0.01	<0.01	NS	NS
Female solicitation call time	0.47	0.53	0.42	NS	NS
Associate with female time	0.00	2.01	1.94	***	NS
(B) Intruder Present					
Intrusion occurrence frequency	3.69	0.07	0.16	***	NS
Repel intruder frequency	0.00	0.07	0.16	***	NS
Total intrusion time	33.20	0.51	0.39	***	NS
Intr. time >5 m between birds	23.53	0.33	0.20	***	NS
Intr. time 0.5-5 m between birds	8.06	0.17	0.19	***	NS
Intr. time <0.5 m and contact	1.61	<0.01	<0.01	***	NS
Primary song (or attempt) time[d]	0.28	2.62	1.56	***	*
Chase time[d]	4.71	2.52	2.86	***	NS
"Alarm/Threat" call time[d]	1.81	<0.01	<0.01	***	NS
"Attack" call time[d]	<0.01	<0.01	<0.01	NS	NS
Wing raise time[d]	4.71	2.52	2.86	***	NS
Grass pick time[d]	0.20	0.00	0.00	***	NS
Sham-preen time[d]	2.65	0.00	0.00	***	NS
Bob and bill jab time[d]	0.14	0.00	0.00	***	NS
(C) Playback Reaction					
Primary song (or attempt) time	3.84	4.71	4.44	*	NS
Tuck, Tsip, Si Twitter time	10.77	12.03	11.11	NS	NS
Tchi-Tyu and Zuck call time	<0.01	0.11	0.08	NS	NS
Tchi flight frequency	0.62	0.86	0.81	NS	NS
Wing raise time	0.79	0.55	0.66	NS	NS
Grass pick time	0.55	0.22	0.36	NS	NS
Sham-preen time	3.41	2.98	3.71	NS	NS
Bob and bill jab time	0.35	0.22	0.41	NS	NS
Latency of reaction time[e]	0.99	0.91	0.88	NS	NS
Within 5-25 m model time	21.11	25.37	23.78	NS	NS
Within 0.5-5 m model time	11.52	10.37	12.21	NS	NS
Within 0.5 m model time	2.71	2.69	3.01	NS	NS
Contact model frequency	0.91	1.11	1.32	NS	NS

Table IV-5--continued

[a]Similar vocalizations and behaviors are grouped: Tuck, Tsip, and Si Twitter calls ("alarm/threat calls") are given in reaction to nearby (0-15 m) predators and avian invaders; Tchi-Tyu, Tchi, and Zuck call ("attack calls") are vocalizations often used by males and females invading another territory; Wing raises, grass picking, sham-preening, bobbing and bill jabbing are visual displays given in the presence of nearby (0-5m) predators and avian invaders.

[b]Figures are mean values per bird for 21 Muted, 13 Sham-Operated, and 20 Undisturbed birds. Minimum observation time per bird was 10 h for (A) and (B). Time results reported as min/h; playback results standarized to min/h. Frequency results reported as mean occurrences/h. Group comparisons tested with two-tailed Mann-Whitney $\underline{U}$-tests. "M/S" compares mute to Sham-Operated groups; "S/U" compares Sham-Operated to Undisturbed groups. Significance of differences between groups: ***$\underline{P}$<0.002; **$\underline{P}$<0.02; *$\underline{P}$<0.05; NS=Not Significant.

[c]Includes countersinging with another males off territory.

[d]Standardized to min/h intrusion.

[e]Minutes from first song on tape to first observed reaction; not standarized to min/h.

Behavior with no intruders present. Singing rate and other

behaviors were measured under two conditions: unprovoked ("no intruder

present") and intruder-induced ("intruder present"). The unprovoked

"song" (attempted song) rate and flight song frequency of Muted birds

was less during their songless state than before they were muted. They

also spent slightly less time giving unprovoked song than Sham-Operated

and Undisturbed birds.

Muted birds spent less time interacting with females while muted

than before. Also, compared with the Sham-Operated group, Muted birds

spent much less time with females. Other behavioral observations

collected under non-intrusion conditions showed no significant

differences between Before and During muted, and no difference between

the Muted and Sham-Operated groups.

Behavior during intrusions. Songless birds experienced major

problems in their confrontations with other males. Normally territorial

boundaries are well established by April. Thereafter, neighboring males

squabble only occasionally, and rarely do floaters (non-territorial

males) challege territorial birds. Territory owners usually react to

intruders by first increasing their singing activity, then if necessary

with short-distance aggressive calls and displays, and infrequently with

physical attack. Frequency of intrusions and behavioral reactions to

intrusion differed considerably for muted birds both in comparison with

themselves prior to muting and in comparison with Sham-Operated and

Undisturbed birds. Invasions into the Muted birds' territories by

neighbors and floaters were immediate, and these provoked heightened

aggressive interactions. Often intruders came in and began to assert

themselves by singing and by associating with the resident females

within several hours after the muting surgery. Muted territory owners reacted to intruders with their most intense and aroused calls and close-range displays. Intruders usually ignored or simply avoided muted birds, or seemingly treated them as mere annoyances.

Prior to manipulations I measured intrusion frequency, total time of intrusion, and birds' behavior during intrusions. I then made Before and During comparisons of intrusion rates and reactions. I compared total time of intrusion, and Before and During changes in four categories of behaviors measured for the 21 Mid-Season Muted birds (Fig. IV-4). Tests of behavioral changes were made with two-tailed Wilcoxon matched-pairs signed-ranks tests (Table IV-4).

Invaders spent significantly more time on Muted birds' territories and none was successfully repelled. While songless, Muted birds reacted to intruders with more chases, "alarm/threat" calls, and close displays (wing raises, grass picking, sham-preening, and bob and bill jabs) than they did before being muted. There was no significant difference in the time birds reacted to intruders with "attack" calls. During their songless state, however, the Muted birds spent less time reacting to intruders with song attempts, compared to the time they spent singing during intrusions before they were muted.

Figure IV-4. Behavioral changes of 21 muted birds Before and During their songless periods. Changes are compared as mean time (min/h) birds were involved in designated activities. The two bars on the left (A) compare the overall time the bird's territory was invaded upon. The eight bars on the right (B) compared (in min/h intrusion) how birds reacted during the time intruders were present. All changes were significantly different (one-tailed Wilcoxon matched-pairs signed-ranks tests), 21 paired observations per test.
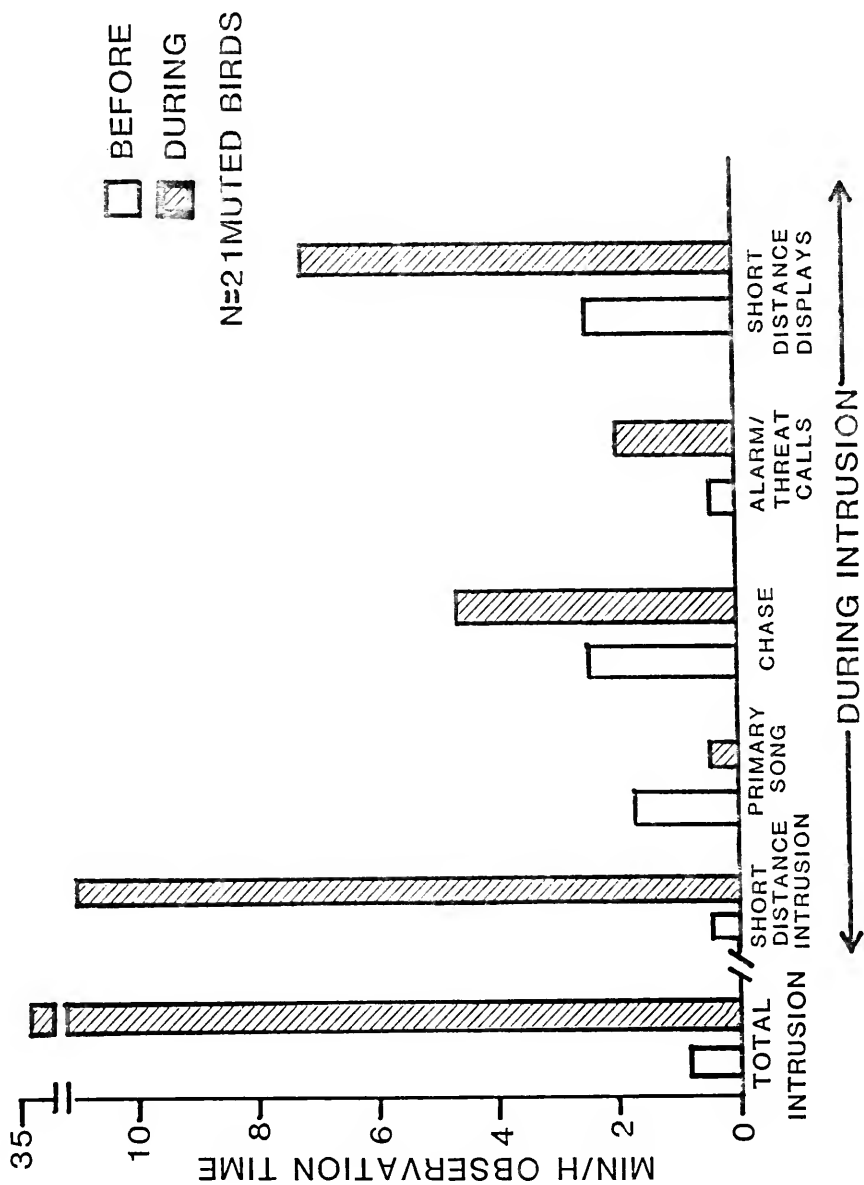
Reaction to Playback

Playback experiments simulated intrusions under more controlled conditions. I compared the reactions to playback of Muted birds before and During their manipulation using two-tailed Wilcoxon matched-pairs signed-ranks tests, and I compared the Mute to Sham-Operated groups with Mann-Whitney U tests. I did not compare statistically the After to Before and During playback reactions because of the end-of-season decline in observable behavior.

Playback experiment results are summarized in Tables IV-4(C) and IV-5(C). For all treatment groups the pattern of reactions to playback was generally similar to reaction to natural intrusion (Tables IV-4(B) and IV-5(B)). Playback stimulated more intensive reaction behavior overall than did natural intrusions. Muted birds responded to playback with "songs" less During muted than Before. Other playback reaction behaviors did not differ significantly between Before and During muted.

Treatment group comparisons (Table IV-5(C)) indicated that Muted birds attempted song less that Sham-Operated. Other reaction behaviors did not differ significantly between Muted and Sham-Operated. For all birds, their reactions to playback both Before and During was generally similar to their reactions to natural intrusions (Table IV-4(B)). Muted birds did, however, react to playback with "songs" slightly less During muted than Before. Other playback reaction behaviors did not differ significantly between Before and During for both treatment groups. Sham-Operated and Undisturbed groups did not differ significantly in any measurement.

Voice Recovery and Subsequent Behavior

After regaining their singing ability in 10-15 days, 8 of the 10 birds muted in the Early Season round eventually acquired mates and territories. Mid-Season Muted birds did not rebound as quickly. Only 2 of these 21 birds re-acquired a mate by the end of the breeding season. Most of these males did, however, regain their own or a new territory by 21 days after muting (Table IV-3).

One year following surgery 14 of the 21 Mid-Season muted birds returned and appeared to function normally in every respect. The numbers of returning Muted (67% of 21), Sham-Operated (62% of 13) and Undisturbed (73% of 30) birds did not differ significnatly ($\underline{X}^2$ 2X3 test, $\underline{X}^2$=0.11, 2 $\underline{df}$, $\underline{P}$>0.7).

Discussion

Singing ability is unquestionably crucial for a male seaside sparrow to attract a mate and maintain a territory. These two proximate functions of song are not, however, mutually exclusive. As discussed in Catchpole (1981), both female attraction and male repulsion are related to sexual selection--the first intersexual, the latter intrasexual. Catchpole proposed that song function may be better represented as a continuum with predicted characteristics of song at each end (Table IV-6). For some species proximate song function is mostly intrasexual, used in male-male interactions. For birds at the other end of the continuum, the primary function is intersexual, used in male-female breeding behavior. This model is relevant to seaside sparrow song. Their singing behavior is a mixture of the characteristics listed in Table IV-6. They sing short, simple songs and sing after pairing. Yet

Table IV-6. Sexual selection related to two main song types

Selection Pressure

Attribute	Intersexual Selection	Intrasexual Selection
Main proximate function of song	Female attraction	Male repulsion
Female choice	Direct	Indirect
Song structure	Long, complex, variable Songs not repeated Continuous singers	Short, simple, stereotyped Song types repeated Discontinuous singers
Contextual correlations	Stops singing after pairing Tend to be migratory	Continues singing after pairing Tend to be resident
Direct effect on males	No matched countersing Little playback effect in repelling rivals	Matched countersing Playback repels rival males from territory
Direct effect on females	Larger repertoires attract females first	Larger repertoires do not attract females first

Source: Adapted from Catchpole (1982)

they are continuous singers and probably do not match songs significantly while countersinging. Experimental results from this study indicate that seaside sparrow singing falls midway along this continium, functionally as well as diagnostically.

Why did muted birds behave differently? Their responses to intruders changed after manipulation, both as compared to themselves prior to muting and as compared to Sham-Operated controls. A normal bird's first reaction to territorial threat is increased singing, and this is usually successful in repelling intruders or intrusion attempts. Because the muted birds' song attempts were ignored by intruders, however, they resorted to more intensive defense behaviors--aroused calls, close-range visual displays, chases, and even contact fights.

These results are consistent with several other ethological studies where removing socially significant signals resulted in animals spending more time and energy in intrasexual conflicts as a response to the behavior of surrounding individuals (Peek 1972; Rohwer 1977). The increased territorial intrusions and behavioral changes of muted seaside sparrows were similar in some respects to the changes described for muted red-winged blackbirds (Peek 1972; Smith 1976; 1979). There were, however, several notable differences. Muting red-winged blackbirds had no apparent effect on their mate-retention abilities. Furthermore, although territorial intrusion rates increased, most males were still able to maintain their territories. Smith (1979) concluded that the visual component of the song-spread display, combined with other visual displays, were effective intruder-repulsion behaviors in red-winged blackbirds.

Smith also speculated that female red-winged blackbirds may also have at least partially chosen males on the basis of their visual displays and their territory quality. Female choice based on resources, the most familiar being territories, is also known in other birds (Selander 1972). Female seaside sparrows, however, deserted the territories of their muted mates within a few days after muting. Most solicited copulations from the nearest persistent singer. Thus female seaside sparrows seemed to be assessing males based on a behavioral characterisitic--singing ability--rather than their territory quality.

Because females of muted males associated with singing males who already had mates, I unintentionally induced temporary artificial polygyny in my study population. I have no data indicating whether the females thus sharing non-muted males were aware of their polygynous condition. If they were aware, then apparently these females were opting to cross the "polygyny threshold" (Orians 1969) and share a mate rather than remain as the exclusive female on a muted males's territory. Apparently for female seaside sparrows, monogamy and mate fidelity are not rigid innate behaviors. The female's immediate choice to associate with a given male seemed instead to be more of a matter of convenience and her attraction to males with greater song output.

Intruding floater males seemed to appear from nowhere after I muted birds. Floaters took over 6 of the 21 Mid-Season Muted birds' territories within hours to several days. Five other floaters wedged themselves into the areas adjacent to muted birds territories, causing these territories to shrink appreciably. Surprisingly, three of the six lost territories were taken over by floaters that had been territory owners at the exact location the year before. Prior to these

experiments, the existence of floater males had not been detected in this well-studied population. Perhaps the existence of floaters in avian populations is more common than generally recognized.

The muting technique described herein has great potential in the field study of bird song. The role of song in duetting species, in determining the relative contribution of parents and neighbors in song learning, and in investigating the relative importance of sexual and territorial functions of song in other species, could all be approached using judicious muting experiments. Also of interest would be studies on visually displaying birds designed to test the relative contribution of acoustic versus visual display in social interactions.

This study has shown that the sound message, the auditory modality of singing behavior (and not the visual component), is critical for a male seaside sparrow to attract a female and maintain his territory. Because "muted" birds did give normal calls and went through the motor patterns of singing, there was an unexpected yet perfect control for comparing "song" to "no song" behavior: the design problem of separating the visual component of the song display from the auditory message was overcome. The effect of the surgery itself was surprisingly minimal, as evidenced by the undaunted behavior of the Sham-Operated birds. This is one of the first well-controlled field studies that clearly substantiates the dual function of song hypothesis--birds sing both to attract females and to repel males. The results clearly show that inability to sing has devastating consequences to a male seaside sparrow's reproductive success.

CHAPTER V
CONCLUSIONS

In this dissertation I have described the reproductive biology and vocalizations of a population of seaside sparrows. I have also reported my experiments on the function of song and have interpreted my findings.

Scott's seaside sparrows at Cedar Key have presumably lived in a relatively stable salt marsh habitat, isolated from human interference, for thousands of years. Thus, it is likely that the birds' reproductive strategies, behavior, and vocalizations are well-adapted to their environment.

Despite considerable nest destruction due to predation and flooding, the population maintained its numbers over the years of this study because of the birds' repeated nesting attempts and their relatively high survival rate.

The seaside sparrow's repertoire of distinct calls and a primary song were used differentially throughout the year. Some vocalizations conveyed general messages, such as alarm; other vocalizations transmitted more specific information, an example being the female's solicitation call. I experimentally determined that the male's primary song had two functions: mate attraction and retention, and male repulsion. My experiments clearly substantiated the "Dual Hypothesis" of song function, which before this project had only been inferred from observational studies.

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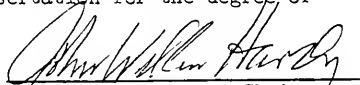Smith, W. J, 1977. The Behavior of Communicating. Cambridge: Harvard Univ. Press.

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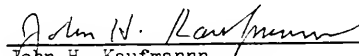
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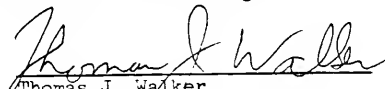
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